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CAPE PROVINCIAL MUSEUMS

— **South Africa** —

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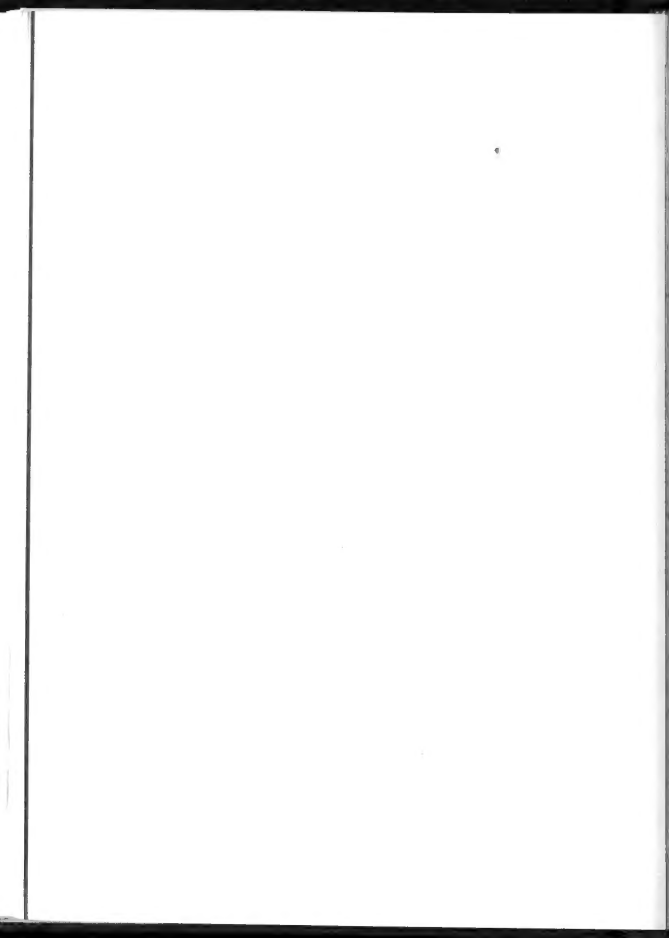
PORT ELIZABETH

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The Annals of the Cape Provincial Museums are published jointly and annually by the five Cape Provincial Museums situated at East London, Grahamstown, Kimberley, King William's Town and Port Elizabeth. The editorial headquarters are at the Albany Museum, Grahamstown. The Journal is intended to record the results of research in the fields of pre-history, cultural history and natural history.

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ANNALS
OF THE CAPE PROVINCIAL MUSEUMS
VOLUME II • AUGUST 1962

PROCEEDINGS

of a symposium on the
CAUSES AND PROBLEMS OF ANIMAL DISTRIBUTION
with special reference to Southern Africa
held at the
MUSEUM, PORT ELIZABETH,
6 to 8 JULY, 1961
under the auspices of the
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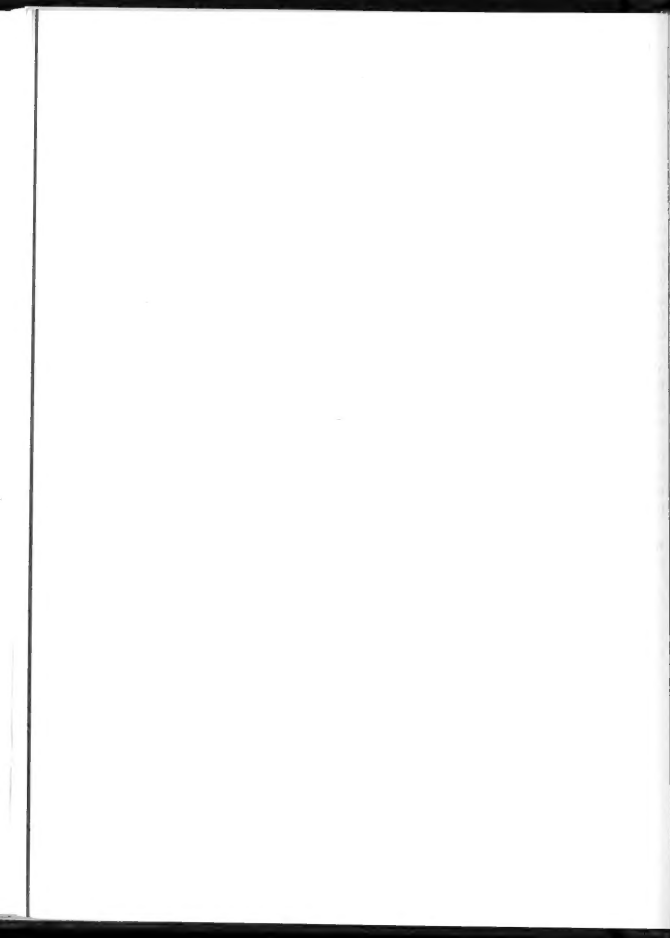
Foreword

On the occasion of its second annual meeting, which assembled in Port Elizabeth in July 1961, the recently-formed Zoological Society of Southern Africa invited its members to contribute to a Symposium on the CAUSES AND PROBLEMS OF ANIMAL DISTRIBUTION, WITH SPECIAL REFERENCE TO SOUTH AFRICA. Twenty-seven papers were presented and these collectively provide a more comprehensive review of modern zoogeographical research in the subcontinent than has ever been assembled before. It is thus with special pleasure that the Council of Society is now able to publish these contributions and make them available to other students in a single volume.

This could not have been achieved but for very liberal assistance from many other organizations and individuals. In particular, we are indebted to the Editorial Board of the Cape Provincial Museums who have generously made available an entire volume of the *Annals of the Cape Provincial Museums* for the publication of these Proceedings. In addition, several other bodies have met the costs of printing individual papers, and for such assistance we wish to extend our thanks to the Council for Scientific and Industrial Research; the Department of Education, Arts and Science; the Natal Parks, Game and Fish Preservation Board; the Transvaal Department of Nature Conservation; the National Institute for Water Research, Pretoria; and the University of Natal.

We would acknowledge also our debt to the Trustees, Director and staff of the Port Elizabeth Museum, Snake Park and Oceanarium for providing a venue for the symposium and for much further hospitality during the 1961 meeting.

Finally, the Council of the Society wishes to record its appreciation of the generous co-operation and assistance received from Dr. T. H. Barry, Director of the Albany Museum, Grahamstown, and Editor of these *Annals*. Without his help at all stages and especially in the final seeing through the press, the prompt production of these Proceedings could not have been achieved.



M. R. (LEVYNS

RONDEBOSCH,
CAPE TOWN.

✓
Past plant migrations
in South Africa ✓

The flowering plants which dominate the world to-day are late-comers on the world's surface. South Africa had its share of pre-Angiospermous floras but little is known of their migrations. The Glossopteris flora which flourished in late Palaeozoic times was widely spread in the Southern Hemisphere but little is known of its fate and whether or not it left descendants to become incorporated in later floras. The Gymnospermous floras of Jurassic and early Cretaceous times probably have left their mark on the present floras but our knowledge is so incomplete that no attempt is made to deal with them here.

The flowering plants or Angiosperms appeared with great suddenness towards the end of the Cretaceous period, having no obvious links with the groups of plants which preceded them. No one knows their origin though many theories have been propounded. As yet no claims have been made for Africa as their homeland which is not surprising as Cretaceous fossils are not well represented here. Furthermore groups of plants which botanists usually assume on morphological grounds to be primitive, such as Magnoliaceae, are conspicuously absent from Africa. This being so, the assumption may be made that flowering plants migrated into Africa displacing the early Cretaceous flora in which they had no part. The obvious question then is: what was their source?

At the present time Africa forms an extension of the northern lands in the Old World. Though the Sahara to-day forms a most effective barrier to migration of plants and animals, this was not always so. In earlier times Africa probably received at any rate part of its population from the north. It has even been suggested that South Africa resembles a vast cul-de-sac into which species from the north poured and, having no outlet, became massed in the extreme south. At one time the unusually large number of species in the Cape Flora was explained in this way. It is doubtful if anyone upholds this view at the present time for it is based on the assumption that the continents have maintained their present outlines and relative position throughout the ages, an assumption that few would be prepared to defend.

Little is known about the climate in Tertiary times. The scanty evidence available suggests that for part of the time the climate was more favourable to plant life than at the present time. Deposits at Knysna and East London indicate that trees were common. Even at Banke in Namaqualand fossils of presumed Tertiary age, recovered from a filled in pipe, indicate that the flora at that time contained trees and ferns of a type which could not exist there at the present time. As so little is known about South African plants of the Tertiary Era, evidence of the conditions in other southern lands becomes important. Recent research

has made it clear that during this period there was a widespread southern flora the remains of which have been and are being revealed in rocks of lands in the south, including Antarctica. In South Africa a few Tertiary plant fossils are known, belonging to genera such as *Podocarpus* (yellowwood) and *Curtisia* (Assegaibos) and many more will doubtless be revealed when modern methods of analysis are applied. Evidence for the occurrence in South Africa of a southern element is based, for lack of anything more positive, on a knowledge of present day distribution. Yellowwoods, Assegaibos, Rooi Els and Wild Almond are likely remnants of an old southern flora. Whether this flora advancing from the south met another angiospermous one of northern origin is not known. All that can be stated is that within the forests and streamsides of South Africa elements of both northern and southern origin appear to have mingled. Forests at the present time are best developed in the Knysna-Humandsorp area but isolated patches of the same type of forest occur in sheltered ravines whenever sufficient moisture is assured. The forest and bush of the coastal strip, in the east show an affinity with the forests just mentioned and they too are likely to contain elements derived from the old austral forests. It may be significant that *Peripatus*, that curious archaic creature in the animal kingdom, is confined to the southern land masses and that it occurs in indigenous, moist forest of the type just assumed to contain remnants of the oldest African angiospermous flora.

A feature which characterises an old flora is that no species appears to be much more numerous than any other. The result is a mixed community. This is the case in the forest flora. It also characterises another assemblage of plants, usually termed the Cape Flora. This is not a forest flora for trees in it are rare. The characteristic life form is that of low bush, the plants having either small flat, leathery leaves or even smaller heath-like leaves. It is a flora rich in species and with many unusual plants. It has attracted the attention of botanists since the discovery of the Cape. This flora with its unexplained links with that of Western Australia, has fired the imagination of many who assumed it to be the remains of an old austral flora. However, evidence for such an origin is lacking. Detailed taxonomic and distributional studies of some of the larger genera have given indications of a possible northern origin. Though its headquarters at the present time lie in the south western coastal belt of the Cape Province, especially those parts with a Mediterranean climate, it has left outliers on high ground throughout Africa as far north as Abyssinia. It is difficult to explain disjunctive distribution of this kind in any way but by postulating a once widespread flora which changes of climate have eradicated from most of the lowlands, leaving evidence of its past history on high ground where the climate permits its continued existence. Some indication of its age lies in the fact that certain elements of the montane flora of Madagascar clearly belong to the Cape Flora and have their nearest relatives on the mountains of East Africa. It is usually assumed that Madagascar became detached from the mainland during the latter part of the Tertiary Era and it is therefore obvious that the Cape Flora must have been in existence before the separation took place. Another significant feature is that tropical African species are usually primitive ones in their respective genera. The most highly advanced species are mostly found in the south-west where there is a striking concentration of species. This concentration of species appears to be a secondary feature and may well be connected with the advent of a mediterranean climate in comparatively recent times. The Cape Flora is probably next in age to the forest flora. It is far more tolerant of moderate drought than the latter and was fitted to survive at times when a dry period challenged the existence of forest in all but the most sheltered places. Little is known of the Tertiary and Quaternary history of South Africa but what is known suggests that there were fluctuations of climate, very dry and somewhat humid periods alternating.

Another notable type of vegetation is what may be termed the Namib-Karoo. It is chiefly developed in the west, extending from South West Africa, through Namaqualand to the coastal ranges which form the boundary of the Cape Flora. It extends eastwards to

about the longitude of Port Elizabeth. In outline its territory is like a somewhat distorted axe standing on its head. In the west the junction with the Cape Flora is usually sharp but in the east the boundaries are much less definite. In places the Karoo approaches true desert but over most of its area it is best described as semi-desert. Succulents form an important element, especially in the west and give this type of vegetation a character unique in the Southern Hemisphere. The Karoo Flora is adapted to a low and erratic rainfall. With increasing altitude and the likelihood of severe frost during the winter, succulents disappear and are replaced by sparse, low bush with grasses occupying the ground between bushes after a rainy period. The past history of this most interesting arid type of vegetation is obscure. There are no indications that it arose anywhere but in South Africa and there are no clues as to its age. It is adapted to life under arid conditions and probably arose in one or more of the dry periods in South Africa's history. It is presumably younger than the Cape Flora for the striking discontinuities in distribution which are a feature of the latter, do not appear in it. Far too little is known about it to hazard a guess as to its age though it is almost certainly older than the floras lying to the north.

Its relations with the Cape Flora in the west are interesting. In a place such as Ladismith at the foot of the Swartberg, the Karoo flora appears adjacent to a major outlier of the Cape Flora. The slopes of the Swartberg are covered with typical Cape vegetation. Just to the south a number of koppies, running from east to west, have a rainfall of approximately 10 in. a year, an amount which is critical for these two floras. Even a change of aspect is enough to determine which of these two floras is to be in possession of the ground. The drier northern slopes are covered with succulent Karoo bushes while the shaded southern slopes have a flora of the Cape type. The sharpness of the boundaries in such places suggests that both floras are old and have reached an equilibrium, each holding its own when its specific water requirements are met.

Both the Cape and succulent Karoo floras agree in being unable to withstand severe frosts. The essential difference between the two lies in their water requirements. Thus in arid periods the Karoo flora would tend to invade the domain of the Cape and in the more humid periods the position would be reversed. Historical migrations of this kind would explain the presence of such typical Karoo plants as *Cotyledon paniculata* (Botterboom), *Crassula rupestris* and *Euphorbia mauritanica* (Geel Melkbos) in present day Cape territory. For instance these plants have a somewhat precarious foothold on the Cape Peninsula where conditions for their existence are not favourable. They are Karoo elements in an area that is now almost entirely populated by members of the Cape Flora. The case of the Worcester—Robertson Karoo is somewhat different. There an island of unmistakable Karoo vegetation is surrounded on all sides by the Cape flora. Here too the explanation may well be that in this restricted area of low rainfall, lying to the south of the Langeberg, remnants of a past invasion may have survived but the mystery remains as to why this flora is confined to rocks of Karoo age.

To the north and east of the three floras just discussed, South Africa is covered by a much younger flora having clear affinities with the vast flora of tropical Africa. It is by no means a uniform flora for at high altitudes where severe frosts are common, it assumes the form of grassland. At lower altitudes and with less likelihood of frost, trees appear and grassland gives way to savanna. A sign of youthfulness, such as a tendency for one species to assume dominance at the expense of the others, is there. It is generally accepted that this is the youngest and it is certainly the most widely spread of the South African floras. The annual rainfall varies within wide limits but it is less erratic than that of the Karoo and occurs during the summer months.

Rainfall and temperature, particularly low temperature, are important factors in determining the type of vegetation in a given area, but at the same time the historical back-

ground cannot be dismissed as unimportant. There have obviously been migrations of considerable magnitude but until South African palaeobotany receives more attention that it has in the past and until more is known of past climates, the subject remains to a large extent in the realm of conjecture.

DISCUSSION

Mr. Skead: What is the relationship between *Daedoxylon* and *Podocarpus*?

Dr. Levyns: None.

Dr. Plumstead: *Daedoxylon* is an Araucarian wood, not represented in the present South African flora.

Dr. Poynton: Can you date the *Podocarpus* forest type? Is it of the same date as *Nothofagus* forest?

Dr. Levyns: Yes.

Dr. Schelpe: The distribution of ferns supports Dr. Levyns' conclusion. The great bugbear in distribution problems is that, once the pattern of distribution has shown migration, it is difficult to decide in which direction the migration has taken place. The cytology of certain ferns, which have a higher chromosome number in the Cape than further north, indicates a northern origin of the flora.

Prof. van Zinderen Bakker: Do the leaves found in the northern hemisphere really belong to the Proteaceae? The evidence seems to be doubtful.

Dr. Levyns: The evidence is, indeed, doubtful.

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The pleistocene environment
in Southern Africa:
Hypothetical vegetation in
Southern Africa
during the pleistocene*

THE PRESENT NATURAL VEGETATION

A "Vegetation Map of Africa south of the Tropic of Cancer" was published recently, together with explanatory notes by Keay (1959), and this serves to provide an excellent summary of present knowledge for this region. Figure 1 is based largely on this map but has been modified in some details where later information is available or where there seem to have been omissions from the compilation. There are also some differences in detail as compared with the vegetation map given by Wellington (1955) but the general pattern is the same and his text and photographs should be consulted for concise data on the vegetation types which are distinguished.

THE PLEISTOCENE VEGETATION

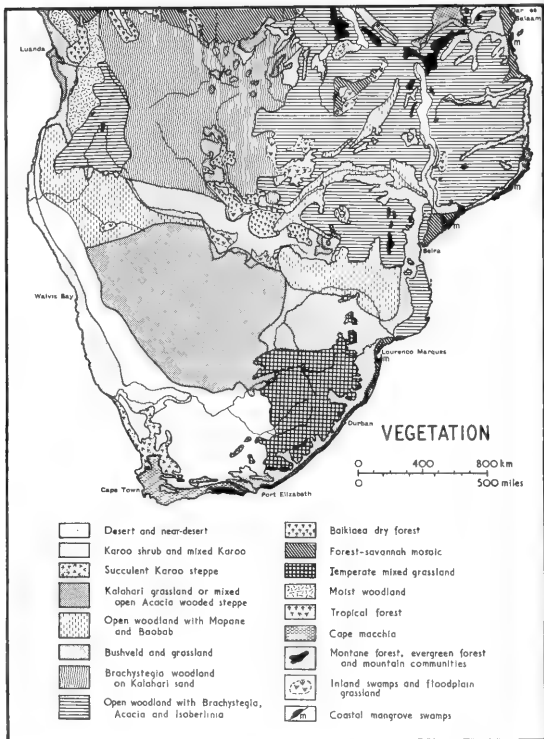
Method of preparing the hypothetical vegetation maps

In preparing the hypothetical vegetation maps it has been necessary to assume that the Pleistocene rainfall pattern accorded with that of the present day as far as the major features are concerned. That this assumption is probably incorrect in detail is freely admitted but it seems to be the best assumption that can be made until the other modifying factors can be estimated more reliably; indeed without this starting point no hypothetical reconstructions can be attempted. In accordance with geological inferences discussed elsewhere (see Cooke *in press*), it is also assumed that the total precipitation varied all over the region from about 60 per cent of its present amount during the dry phases to about 140 per cent during the wet periods. No account is taken of any possible northward extension of the winter rainfall belt and the superimposed effects of temperature are ignored so as not to introduce additional complications. If, as is likely, the actual temperatures were higher during the dry phases and lower during the wet ones, these changes would increase still further the trends of the vegetation patterns away from that of the present day.

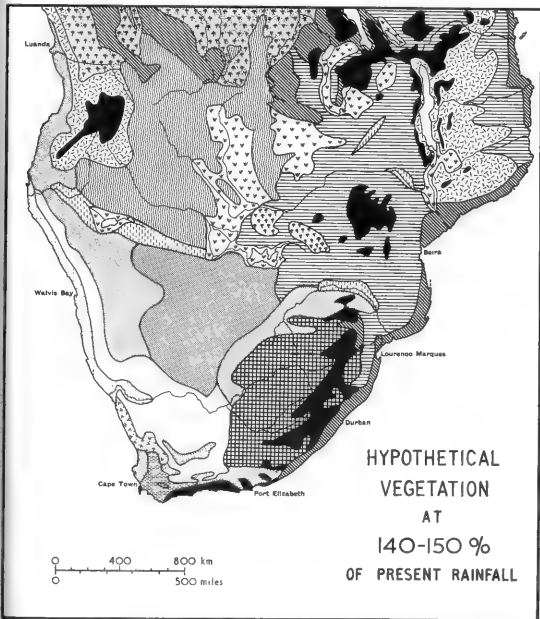
Before constructing the hypothetical vegetation maps, an analysis of the present vegetation was made for the purpose of evaluating the factors which appear to control the distribution of each of the present vegetation types, including rainfall, surface temperature, temperature range, altitude and geological or soil features . . . Two hypothetical rainfall maps

* Extracts (with three vegetation maps) from "The Pleistocene environment in Southern Africa" to appear as the first chapter to *Ecology in Southern Africa* to be published by the Dr. W. Junk-Publishers, The Hague and reproduced here by courtesy of the publishers.

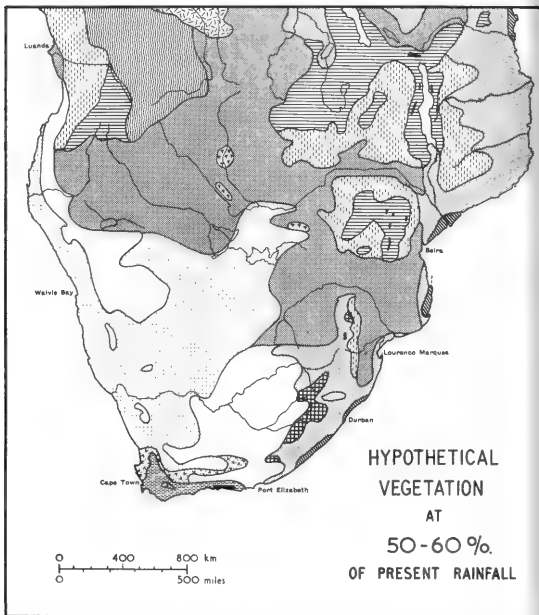
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HYPOTHETICAL VEGETATIVE ENVIRONMENT IN PLEISTOCENE SOUTHERN AFRICA



were then drawn with isohyets based on 140 per cent and on 60 per cent of the present values respectively. Each of these was then superimposed on the unaltered maps of surface temperature etc. and hypothetical boundaries were drawn for each vegetation type on the basis of the criteria previously determined. Every effort has been made to keep the interpretation as objective as



possible and to avoid taking into account the views of botanists on the supposed trends of the natural succession. It must be emphasised that the object is to indicate the *kind* of change in the vegetation which might be expected to result from increased or decreased rainfall and not to claim a precise reconstruction of the actual vegetation during the Pleistocene.

Hypothetical vegetation at 140–150% present rainfall (Fig. 2)

Comparison with the present vegetation map shows no startling features although there is a considerable amount of change in detail. Particularly marked is the apparent effect on the forest areas, which are greatly expanded and extend to much lower altitudes than at present. It is to be expected that the wet valleys would also have carried long tongues of forest far beyond the borders of the forest areas themselves. Another feature is the considerable southward extension of the area suitable for *Brachystegia* vegetation, which might have penetrated the eastern Transvaal lowveld and even northern Natal. Moist woodland would have replaced much of the *Brachystegia* type in northern Mozambique and southern Angola, while tropical forest extended towards the watershed of the Congo basin where the Kalahari sand is not present. The areas suitable for mopane seem to be much reduced. It would also seem likely that large areas of swamp and floodplain grassland would have occurred in Northern Rhodesia. The area of Kalahari grassland is diminished and the South West African highlands off the sand area could have supported bushveld and grassland.

Hypothetical vegetation at 50–60% present rainfall (Fig. 3)

The inferred pattern is rather startlingly different from that of the present day, particularly in the southern Kalahari region where the precipitation falls to marginal levels and suggests the existence of near-desert conditions. The *Brachystegia* areas are greatly diminished and there is a correlative expansion of the mopane and baobab vegetation. The area suitable for temperate mixed grassland is greatly reduced and the evergreen and montane forests would apparently be restricted to small residual patches and to protected valleys. It would seem likely that the thornbush and grassland normally characteristic of the Bechuanaland area would have spread far northwards to replace *Brachystegia* vegetation over most of the Kalahari sand region. It would also appear that much of the area now occupied by bushveld and grassland or mopane and baobab would have been more suited under these conditions to the type of vegetation now growing in Bechuanaland, despite the absence of a sand blanket. The area of the Cape macchia would be little affected owing to its great tolerance of environmental conditions but a considerable part of the area would have been intermingled with succulent vegetation. The reduced rainfall doubtless served also to eliminate most of the swamp areas and perhaps desiccate the minor lake basins. Over a very considerable part of the region under these conditions surface water would be scarce and much of it seasonal in character.

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DISCUSSION

Dr. Brain: The tendency in the past has been to over-emphasise the degree of the change in the rainfall in the Pleistocene. What evidence we have is that it may be of the order of 25 per cent either way but probably not as large as 50 per cent, as in Dr. Cooke's map. Furthermore these changes appear to have been of brief duration, so that it is unlikely that vegetation would have reached an equilibrium as complete as suggested by the maps. This is particularly the case with recent changes, which might have lasted c. 25–30,000 years. The first pluvial may have lasted twice or three times as long, but the evidence for this is not conclusive.

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Botanical evidence
for quaternary climates
in Africa

INTRODUCTION

The distribution of living organisms is, to a great extent, determined by the trends of evolution and by former and present climates. Plants in particular are very sensitive to climate and with sufficient knowledge of plant ecology we can use a vegetation map to obtain valuable information on the complex of factors which is known as "climate". Climatologists therefore make much use of vegetation maps and compare their climatic regions with the vegetation pattern. Land animals depend, directly or indirectly, so much on plant life that their distribution often coincides closely with that of plant communities.

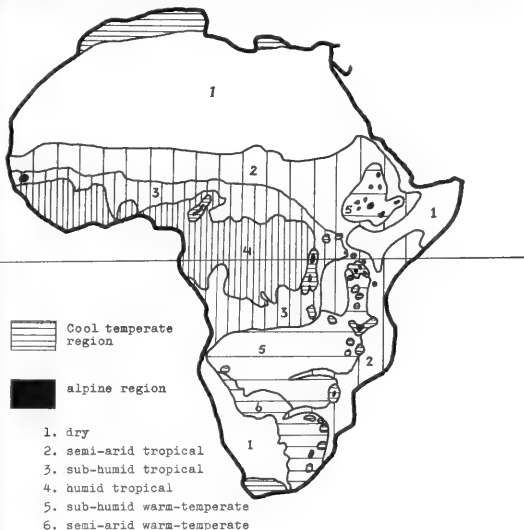
Before considering the relation between climate and plant distribution in former times, we will pay attention to the present-day problem. In analysing the relation between climate and the vegetation pattern we have mainly to consider humidity and temperature. These are determined by many causes such as solar radiation, latitude, cloudiness and a great variety of other factors which depend on the characteristics of the locality. The fact that temperature and humidity are to a great extent interdependent makes it impossible to separate their respective influences in plant ecology. This difficulty has also been encountered by climatologists who try to express the climatic factors in formulae with which they make their maps of the climatic regions, closely resembling the vegetation maps. These classifications accept the plant as a "meteorological instrument" which is capable of measuring all the integrated climatic elements (Trewartha 1954). The climatic classifications of both Köppen and Thornthwaite are not entirely successful from the botanist's point of view (Schulze 1947). I wish to mention a few examples to illustrate this. The big region of the dry hot steppe climate of Köppen (B. Sh. w.) and Thornthwaite (D. B'd.) is not a natural unit as it covers the Kalahari thornveld, the Mopane area, the sweet grassland and also the false Upper Karoo (Acocks 1953). This region should certainly be subdivided (Schulze, *loc. cit.*). Other discrepancies in the classification of Köppen are found in the wide woodland belt which crosses Africa south of the equator and in both systems there are inconsistencies in the area of southern Ethiopia and northern Kenya.

The climatic regions described for South Africa by Jackson (1951) generally give a better approximation of the botanical areas than the above-mentioned systems. The maps of Köppen and Thornthwaite certainly do not correspond well with the vegetation map published in 1959 for Africa south of the Tropic of Cancer (Keay 1959). But our vegetation maps also

have their shortcomings. One of these on the last-mentioned map is the fact that the tropical lowland climate of the Moçambique plain is not clearly shown on it because the woodland belt, which also covers this area, is not sufficiently subdivided.

CLIMATIC CHANGES INFERRED FROM THE PRESENT DAY VEGETATION PATTERN

The problem of describing present-day climate using the evidence provided by the vegetation pattern has not yet been solved as the vegetation shows a great variability and a refined



MAP I · THE PRINCIPAL CLIMATIC-ECOLOGICAL REGIONS OF AFRICA.

sensitivity for the complex factors of climate. A detailed study of plant distribution however reveals a considerable number of "irregularities", which give convincing indications for the understanding of the dynamic nature of climate. Our discussion will try to throw more light on those changes in climate which have especially occurred during the Quaternary. This evidence is strongly connected with plant migration, a subject which has been treated in a separate contribution to this symposium.

For our considerations it is important to recognise only the main climatic regions with special reference to plant ecology. Without going into details, such as the seasonal distribution of rainfall, these regions can be characterised as follows (Map I):

	Precipitation in mm. per annum	Mean July temperature in °C
Dry	<250	—
Semi-arid tropical	250—1,250	≥18
Sub-humid tropical	1,250—1,500	≥18
Humid tropical	>1,500	>20
Sub-humid warm-temperate ..	500—1,250	<18
Semi-arid warm-temperate ..	250—500	<18

Two other climatic-ecological regions are more difficult to define in terms of temperature and rainfall. They are: The *cool temperate region* which includes the winter rainfall areas and the habitat of the temperate and montane forests; and the *alpine region* on the mountains above the tree-line.

Some of the important floras of which elements occur in Africa are the following (Map II):

The Palaetropical Flora of Africa, which inhabits the tropical, the warm-temperate and the desert regions. Many elements of this flora will most probably belong to the autochthonous flora of Africa and can therefore, in accordance with the proposal made by Burbidge (1960) for Australia, be named the *priscotropical African Flora*.

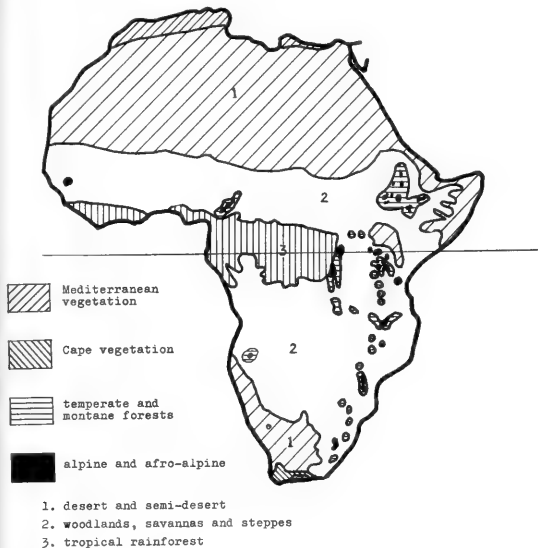
The Mediterranean Flora, which occurs in the cool-temperate region along the northern coast of Africa. This flora is not related to the proper African flora, but to the arcto-tertiary flora of the Northern hemisphere.

The Cape Flora, which is a rich sclerophyllous flora and the southern counterpart of the Mediterranean flora. Two elements of this old flora, the Proteaceae and the tribe Ericaceae of the Ericaceae family, are important for our climatic considerations and will be discussed.

The Montane and Temperate Forests occur in isolated patches from the coast of the Cape along the eastern escarpment northward, where they merge into the montane forests. It is not customary to consider these forests as one entity, but we wish to treat them together, because they show taxonomic affinities and because they prefer a climate which is moister than that of the Cape Flora (Aubreville 1949). These forests show affinities with the Holarctic region, with the African humid tropical region and probably also with Antarctica.

The Alpine Holarctic Flora, of which elements are mainly found on the mountains along the eastern side of the continent as far south as Basutoland; and few of them spread further south into the cool temperate region. These Holarctic genera live isolated in the greater part of Africa as there does not exist a continuous high mountain range as in America. They must be of Tertiary age.

The Semi-desert Karoo Flora is supposed to be of a mixed origin. The affinities of this flora, which is rich in undershrubs, point more to the Cape Flora than to the tropical African Flora (Acocks 1953).



MAP II SOME IMPORTANT VEGETATION TYPES OF AFRICA.

These floras form at present the pattern of the African vegetation. During Quaternary times these floras changed their areas very often. they advanced and retreated, and consequently possess many relic and pioneer stations outside their proper continuous areas. The climatic inference which can be made from the occurrence of these disjunct little areas will be discussed now.

With regard to the *Palaeotropical Flora of Africa*, the tropical rain forest gives the best example for our discussion. A great number of isolated rain forest clumps occur in the sub-humid tropical region in Angola, Northern Rhodesia, Tanganyika, Uganda, etc. These patches show clear affinities to the tropical rain forest and mostly occur at sheltered positions, along drainage systems and near swamps. They are even sometimes found at higher altitudes outside the tropical region in the sub-humid warm-temperate area. Their composition and ecology is entirely different from that of the surrounding dry tropical woodland (Trapnell 1953).

These rain forest clumps are relics of former wetter conditions during the Quaternary and are rapidly disappearing through human influence. Their history can probably be studied with the help of pollen analysis coupled with radio-carbon dating.

The *Mediterranean Flora* is sharply separated from the flora of Central Africa by the Sahara desert and only very few elements have passed this barrier and entered the equatorial region of Africa. Remnants of this flora however still occur in very isolated localities in the desert. During late Quaternary times, until only a few thousand years ago, the desert was however covered over vast areas with a sclerophyllous Mediterranean vegetation. The small refuges, which still exist, indicate a recent desiccation.

A number of genera of the *Cape Flora* are found widely scattered along the eastern escarpment and on the mountains and plateaux of East Africa but some also occur isolated in S.W. Africa (Rennie 1935), in Angola and West Africa. The origin of this flora has been much discussed in recent times (Beard 1959, Good 1953, Levyns 1952, Adamson 1958 and 1959).

Two elements of this flora will be considered in some detail: the Proteaceae and the tribe Ericaceae.

The Proteaceae can be divided into two subfamilies. The subfamily Persoonioideae which occurs in the temperate regions of Australia and Africa differs from the more tropical subfamily of the Grevilleoideae. This last mentioned subfamily is found in South America, N.E. Australia and other eastern territories.

There is much controversy about the origin of this family (Levyns 1958, Vogts 1960, Beard 1959). The idea of a northern origin of the Proteaceae has been put forward on several occasions, but the evidence supporting this theory is not convincing as far as fossil leaves, fruits and pollen grains are concerned (Burbidge 1960, Kräusel 1958, Good 1953). Recent finds of fossil pollen in Russia have not yet been published (personal communications by Mrs. M. M. Vogts and Mrs. S. Samoilovitch).

The distribution pattern of this family strongly indicates a southern origin from the Antarctic continent. The subfamily Persoonioideae is of Afro-Australian affinity. The description of its dissemination in Africa by Beard (1959) gives a clear picture of the origin of its present area in Africa. The less highly developed types have a continuous distribution in the vast woodlands of Southern and East Africa and in the East African montane vegetation belt. They only avoid the deserts, semi-deserts, the humid tropical region and the temperate grasslands. This fact gives us little opportunity for climatic indications of fossil and recent material, as they inhabit a wide range between 1,200 and 3,800 m. altitude. The final migration of the African Proteaceae to the S.W. Cape, where they developed a secondary centre, has been made very acceptable by Beard (1960) and Levyns (1958).

Other elements of the Cape Flora, such as the tribe Ericaceae, are much more important for climatic inference. The origin of this tribe could have been in tropical Africa (Good 1953). This point will only be better understood after the distribution and cytotaxonomy of the ca. 16 Central African species will have been studied.

More than 600 species of this tribe occur at the S.W. Cape. Here they grow down to sea-level, but further north the related species grow at much higher altitude. In the Drakensberg they occur above 1,000 m., in Rhodesia their minimum altitude is 1,300 m., and in Southern Tanganyika they are a typical feature of the vegetation wherever the country reaches an alti-

tude of at least 2,000 m. In East Africa the montane forest favours the same altitude as the Ericaceae and these are therefore found in two belts: scattered below the forest at about 2,000 m. and in bigger concentrations above the forest at altitudes between 3,300 and 4,700 m.

The Ericaceae are thus plants with a narrower ecological amplitude than the Proteaceae and are consequently of greater importance as climatic indicators. They are chiefly confined to the cool-temperate and alpine habitats and occur only scattered in the sub-humid warm-temperate region. Their isolated occurrence, as for instance in many relic stations in Tanganyika, clearly point to former wetter and cooler conditions during the Quaternary.

Many relics of the *Montane and Temperate Forests* still occur from the Knysna forest at the southern coast of the Cape Province northward along the eastern escarpment. These forests are for instance found in the Drakensberg, Inyanga, the Pungwe Mountains and on the isolated volcanoes along the rift valleys. In East Africa the montane forest is sandwiched in the Ericaceous area and usually dominates on that part of the mountain slope which has a cool-temperate climate and which receives the maximum rainfall. The small forest clumps which still occur on some mountain ranges in Northern Rhodesia, as for instance near Mpika at 1,900 to 2,000 m., and in Southern Tanganyika at 2,100 m., are striking examples of a dwindling vegetation type, which is entirely different from the surrounding dry woodland. The same trend of desiccation during the post-Pleistocene is indicated by the clumps of *Arundinaria* which are found scattered in the woodland of southern Tanganyika at about 2,000 m. altitude.

Moreau (1933) has studied the possible former greater area of these forests during more humid periods in East Africa in connection with zoogeography.

Regarding the *Alpine Holarctic Flora*, in the afro-alpine flora of East Africa a number of genera which are of boreal affinity, occur such as: *Delphinium*, *Dipsacus*, *Bartsia*, *Anthriscus*, *Valeriana*, *Epilobium*, *Carduus*, *Crepis*, etc. (Engler 1892, Hedberg 1957). In the alpine region of Basutoland we find species of *Myosotis*, *Ajuga*, *Bromus*, *Hypericum* and *Cerastium*, which are also of northern origin.

The number of northern elements in the vegetation of the high African mountains, especially in East Africa, is much bigger than the number of Cape plants. This could indicate that the Cape Flora was not able to adapt itself so well to the alpine conditions.

According to the speciation which took place, these alpine elements must be very old. Because of their strict isolation, they possess no advance or relic stations but pollen analysis may be able to use these elements as climatic indicators.

The many patches of *Semi-desert Karoo Flora*, which occur north of its present area as far as the northern Orange Free State, have often been used as an indication of desiccation. It has been made very plausible that human influences played a strong part in this rapid northward advance of the Karoo in historic time. During the many arid periods which occurred in the Tertiary, the Karoo Flora must have been widespread in Southern Africa (Acocks 1953).

The above-mentioned evidence indicates that the more humid vegetation types have been retreating during the latter part of the Quaternary. The Cape and Mediterranean Floras, the tropical rain forest and the montane and temperate forests, all left relicts in their wane. Warmer and drier climatic oscillations must have been responsible for this general reaction of the vegetation.

STUDY OF FOSSIL POLLEN (MAP III).

The study of plant geography can supply us with strong evidence for former climatic changes as we have seen in the discussion about relic vegetation, but the time and the extent of these changes is very difficult to assess. Study of fossil pollen should give more accurate information on the time and nature of the climatic oscillations, if only more pollen-bearing



MAP III. LOCALITIES OF FOSSIL POLLEN SITES.

deposits were available. Climate in Africa is, in general, not favourable for the preservation of fossil pollen and shorter or longer periods of dryness have destroyed much valuable material. Pollen is, however, well preserved in wet deposits round permanent springs and in moist mountain regions. The difficulties in explaining former climates with the aid of palaeobotany are more complicated than the analogous recent problems, because in this case it is not only the climate which is unknown, but also our knowledge of the site itself raises specific problems. The site may have been a niche with a vegetation which was not representative of the former

general climate; or the assemblage of fossils may represent only a stage in the succession of the vegetation and not the climax vegetation. So far a limited number of analyses have been made and it should be borne in mind that these first results have only a limited application as they are too far apart to allow valid detailed conclusions. I will discuss the palynological evidence as far as it is available for Africa.

The high mountains provide a very important starting point in East Africa, where pollen-bearing deposits occur and where the pollen diagrams can be coupled with the glaciology of the mountains. Several palynologists are at present engaged in this area. The results can in future, with the aid of C-14 determinations, be correlated with the sequences obtained from the bottom deposits of lakes in the rift valleys and also with the known sequence of the northern hemisphere (van Zinderen Bakker 1958 and 1960).

The coastal lakes and lagoons where sea transgressions can be used to make world-wide correlations form another important starting point (Martin 1959). Inland deposits have to be calibrated with known geological or archaeological sequences or with C-14 chronology in order to be able to compare their pollen diagrams with those of other areas.

The results of East and Central African palynological research have not yet been published, but are promising for the watershed between the Nile and the Congo west of Lake Victoria, and also for the high Kenya mountains. At Kaisungor in western Kenya a mountain swamp is at present being investigated by the author. This swamp which is to-day situated in the upper reaches of the montane forest, started to form when the surroundings were practically treeless. This change in vegetation indicates a decrease in temperature. It is a common feature of the climate of East African mountains that the highest rainfall usually occurs in the montane forest belt, because of the maximum condensation of moisture in the upward moving air at that altitude. Below this belt the precipitation is usually much less, and above the montane forest the rainfall diminishes gradually, so that under special circumstances, as on Kilimanjaro, even desert conditions can occur. The details in rain distribution of course depend to a great extent on the exposure of the site under consideration and on the wind regimen.

A depression of the tree-line indicates a lower temperature and consequently drier conditions in the upper forest limits and in the Ericaceous belt. An upward shift of the forest, as was found in younger deposits at Kaisungor, therefore indicates a rise in temperature.

More evidence for a former lower temperature has been found during the preliminary investigations of the Kalambo deposits, near the southern end of Lake Tanganyika. The excavations, which have been carried out by Clark (1960 and personal communication), provide a wealth of archaeological material and also pollen-bearing deposits. The cooler conditions on this site lasted, according to C-14 age determinations, from at least 57,000 B.P. (before present) to 12,000 B.P. The lower temperature indicated by a number of plants coincided with locally wetter conditions. This fact could be explained by lessened evaporation and also by a downward shift of the vegetation belt, which brought the site temporarily near the belt of maximum rainfall.

Another proof for a decrease in temperature was found in N. E. Angola near Mufo. This material, which was also submitted by Clark, indicates a climate which was decidedly cooler than that of to-day. Mufo is situated at about the same latitude as Kalambo, but at an altitude of 750 m., whereas Kalambo lies at 1,260 m.

The cool periods at Kalambo, and probably also at Mufo, belong to the late Upper Pleistocene. Very interesting evidence on this same period has come to light in Tunisia and the Sahara. Deposits formed round artesian springs in Tunisia contained a pollen assemblage which is not fundamentally different from the present day pollen spectrum of the surrounding steppe. A number of grains however indicate a climate slightly cooler and a little more humid than that of to-day. This so-called "pluvial" is of Würmian age. The "interpluvials" were drier and hotter (Leroi-Gourhan 1958, van Campo 1958? and 1959).

Even on mountains in the central Sahara interesting proof has been found of a cooler and more humid climate during the late Upper Pleistocene. Pons and Quézel (1957) describe indications of a hygromesophyll forest with some *Alnus*, *Fraxinus* and *Tilia* for the Hoggar Mountains.

In postglacial times meso-xerophyll elements of the Mediterranean, semi-arid flora were widespread in the Sahara and North Africa (Hoggar, Tefedest, Mouydir, Tassili 'n Ajjer). Most of these plants disappeared when the desiccation set in about 3,000 years ago (van Zinderen Bakker 1958, Pons and Quézel 1957). The same workers analysed *Procavia* excrements from the Hoggar Mountains in the central Sahara. Although this material is not likely to provide a representative pollen spectrum, it nevertheless shows that 4,680 years ago a Mediterranean flora existed on these desert mountains (Pons and Quézel 1958). According to Hugot (personal communication), a similar pollen spectrum of Neolithic age from the Air has recently been dated at Saclay at $5,140 \pm 400$ B.P.

The pollen content of diatomites from the Tibesti Mountains in the eastern Sahara has also been studied. The pollen of these deposits, which are supposed to be less than 10,000 years old, indicates that a tropical flora lived in the valleys while the summits were covered with a forest of trees from temperate regions, such as *Cedrus* and *Pinus* (van Zinderen Bakker 1958).

Right at the other end of the continent Martin (1959) has studied a pollen sequence of the same age of Groenvlei, a coastal lake between George and Knysna, near Cape Town. Foraminifera and marine diatoms which were found in the lower horizons clearly show a marine transgression with a rise in sea level of ca. 3.3 m. This transgression must have occurred between $6,870 \pm 160$ and $1,905 \pm 60$ B.P. and could very well be contemporaneous with the Atlantic transgression in north-western Europe during the climatic optimum. The pollen indicates that until the return of freshwater conditions a heath vegetation with a climate similar to that of today existed. After that the coastal woodland became more important which indicates a higher rainfall. The climate of the coastal region of the Cape may not have changed considerably since the Middle Pleistocene, but it is important to know whether the temperature and humidity changes were contemporaneous with those of the interior of the continent.

The only pollen diagram which has been published from the interior of Southern Africa is that of Florisbad (van Zinderen Bakker 1957). This site, which became famous because the skull of *Homo helmei* and much palaeontological and archaeological material were found here, also provided pollen-bearing deposits of special interest. The oldest peaty layers, near the human skull, indicate a warm, semi-desert climate with a rainfall of about 125 to 250 mm. per annum. As the present-day rainfall in the Florisbad area varies between 450 and 500 mm. the lowest peaty horizon must have been formed during a nonpluvial which is, according to C-14 determinations, more than 43,960 years old. The pollen diagram shows in the younger part a change to a slightly wetter climate, above which it is interrupted and pollen is only found again in younger deposits between $28,460 \pm 2200$ and roughly 19,000 years ago. The climate as indicated by the pollen preserved in these late Upper Pleistocene layers began oscillating between wetter and drier conditions. The treeless vegetation gradually merged into a grassland, which could have been the warm-temperate grassland as is at present found on the plateau round Bloemfontein in the Orange Free State. It is however more likely that it was a mountain grassland of the cold alpine type as occurs at present in the Drakensberg above the tree-line. It is difficult to prove which type of grassland is presented in the pollen diagram. The change to alpine grassland would mean a considerable increase in humidity and a big drop in temperature.

Florisbad provides good evidence for an important change in climate during the Upper Pleistocene, causing the dry Karoo vegetation to give way to a much wetter temperate or

alpine grassland. Many patches of Karoo vegetation which are at present found as far north and east as the line Lichtenburg-Heilbron-East London are indications of the slight equilibrium of this vegetation, which can easily turn either way. (Acocks 1953).

QUATERNARY CLIMATES

The Quaternary period was marked by extensive glaciations which are best known on the northern hemisphere. The sequence of four major glaciations has been substantiated, especially in Europe, by comprehensive geological, palaeontological, botanical and archaeological evidence. The chronology thus established has been supported by many dating techniques of which the modern C-14 method gives convincing proof of the exactness of the younger part of the time scale. In future the Potassium-Argon method will probably contribute substantially to the dating of the Middle and Lower Pleistocene. The temperature curves published by Gross (1958) and Woldstedt (1958) give representations of the three main sections of the last glacial, the Würm, and its many oscillations. Gross and Movius (1960) have published reviews about this period.

The last Quaternary glaciation is the most important for our present discussions and we may summarise its sequence as follows (Table I).

The preceding interglacial, the Eemian (Riss-Würm), was a period with a climate warmer than that of the postglacial and marked by a high ocean level. The first phase of the glacial, the cool humid Early Würm, ended about 47,000 years ago, when the Göttweig Interstadial began. This warmer period lasted for about 18,000 years and was followed by the Early Phase of the Middle Würm. The warmer Paudorf Oscillation, about 26,000 years ago, separated the Early Phase from the Main Phase of the Middle Würm. The Würmian glaciers had their maximum advance in this phase during the extremely cold and dry Brandenburg Stadial, which occurred about 18,000 to 20,000 years ago. Since then the climate has ameliorated gradually, but the Late Würm had again two major warmer oscillations, the Bölling and the Alleröd, at about 15,000 and 12,000 years ago, respectively. The last 10,000 years since the end of the glacial are mainly marked by the Hypsithermal Interval which coincided with a high ocean level between 9,000 and 2,600 years ago. (Flint 1957).

This climatic chronology, set up for Europe can, in general, be applied to other parts of the northern hemisphere. Evidence gradually coming from America shows remarkable similarity (Flint and Brandtner 1961). Very interesting in this respect are some of the results of the research done on the stratigraphy and pollen sequence of Pleistocene lake sediments in the Searles Basin by Flint and Gale (1958). The Wisconsin glaciation of Northern America was here found to be contemporaneous with a cooler, pluvial period, which began more than 23,000 years ago and lasted till about 10,000 years B.P. This youngest pluvial period of Searles Lake coincided also with the severe glacial of the Middle Würm and with the Late Würm in Europe. An earlier pluvial was roughly coeval with the Göttweig Interstadial in Europe. Fossil pollen and fossil aquatic molluscs indicate for these pluvials a decrease in temperature of probably 6 to 8° C.

Very important support for the hypothesis of a general decrease in temperature during the late Upper Pleistocene, even in the tropics, comes from Colombia (S. Am.) from the study of fossil pollen and geological data by Maarleveld and van der Hammen (1959) and van der Hammen and Gonzalez (1960). The pollen diagram of a core of 32 metres of chiefly lake sediments has been used for the construction of temperature, tree-line and precipitation curves. The Upper Pleistocene and Holocene section of the curves has been calibrated with radio-carbon dates.

The remarkable fact is that glacial and interglacial periods, which were contemporaneous with those in Europe, were found in the Andes at an altitude of 2,560 m. The temperature curve in general fits well with the curves published for the Würm by Woldstedt (1958) and

TABLE 1:
WÜRM-CHRONOLOGY AND RADIO-CARBON DATES
(acc. to Gross 1958)

Post Glacial			Radiocarbon Dates B.P.
Main Würm	Late Würm		10,000
		Alleröd Oscillation	12,000
		Bolling Oscillation	15,000
			ca. 17,000
	Main Phase		
	Paudorf Oscillation		25,000
	Early Phase of Main Würm		26,000
			29,000
Göttweig Interstadial			
			ca. 47,000
Early Würm			
Eemian = Riss-Würm Interglacial			

Gross (1958). Temperatures during the maxima of the Würm were 7°–8° C lower than today. During the warmest phases of the interglacials the temperatures were about 2°–3°C higher than at present.

The glacials in the South American tropics were periods with a higher precipitation. The late Würm was relatively dry. A lower temperature caused a downward shift of the tree-line, but a higher annual precipitation forced it upward. During the last maxima of the Würm the tree-line was about 800–1000 metres lower than to-day.

The pollen studies of Auer (1958) in Fuego-Patagonia also indicate a low temperature and a glaciation for the southern end of South America during the Würm.

Interesting evidence for Quaternary climates has also come forward from the studies of Emiliani (1955, 1958) on fluctuations of isotopic-temperature in deep-sea cores in the tropical Atlantic ocean. The results show that the temperature minima fit well with the maxima of the Riss and Würm glacials. The isotopic temperatures from sea-floor sediments suggest that the surface water of the Pleistocene tropical Atlantic ocean was approximately

6° 8°C. colder than to-day. These results are of very great importance as they also point to a general decrease in temperature during the Ice Ages, even in the tropical oceans.

DISCUSSION

The foregoing records from other parts of the world have been enumerated in order to compare them with the data available from pollen sequences in Africa. Surveying the evidence provided by fossil pollen in Africa we see that scattered but consistent proof points to a lowering in temperature during the late Upper Pleistocene on the whole continent. This drop in temperature was generally not high. In East Africa a downward shift of the higher mountain vegetation belts of at least 500 to 600 m. can be visualised. This would imply a decrease in temperature of at least 3°C. Flöhn (in Woldstedt 1954) estimated the decrease in temperature in the tropics during the glacial period at 4°C.

I will try to give a general picture of the climatic changes which may have occurred under these circumstances in different areas in Africa.

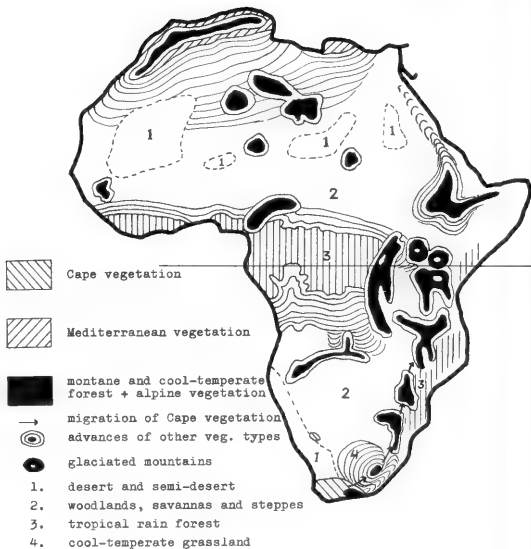
The Mediterranean area was probably directly affected by the cold climate of the European continent. The region at present receives its winter rain mainly from the depressions which travel from the Atlantic Ocean eastward. These cyclones must generally have passed much further south than to-day, because their northern tracks were closed by the ice-sheets and the glacial anticyclones, which occupied them (Zeuner 1959). Many more depressions must have travelled over the Mediterranean from west to east and brought a higher rainfall to this area. Their influence must even have reached far into the Sahara and have supported the distribution of mesohygrophyll forest on the desert mountains and sclerophyll *macchia* elements in the true Sahara.

The position in the S. W. Cape area is largely identical with that of the Mediterranean region. The southward movement of the high-pressure belt of about eight degrees in summer is at present partly responsible for the dry summer weather (Meteorological Service, R.N. and S.A.F. 1948). A northward movement of the high-pressure belt during a maximum of glaciation in Antarctica could have been responsible for a displacement of the tracks of the cyclones to lower latitudes, which would have brought more rain to the Cape area. It will be necessary to obtain pollen evidence and C-14 dates from the S. W. Cape area in order to establish how these cold and more humid periods fit in the Quaternary chronology.

The mountain areas in Africa must have been influenced differently by a lowering in temperature. A decrease in temperature should have had a direct influence on the condensation of moisture in the upward moving air, as already discussed. The maximum of condensation moved downwards and consequently lowered the montane forest belt. Lower regions, which formerly received less rain, had an increase in precipitation, because of this shift, while higher altitudes dried out more. Such a shift in the rainbelts had a much bigger influence than the slight decrease in temperature on the tree-line of montane forest, and the sclerophyll vegetation of the *Ericaceous* belt must have taken the place of the upper forest.

Higher up the mountains the decrease in temperature lowered the line of maximum snowfall and contributed to the growth of the glaciers on the highest mountains. It is therefore supposed that the cooler period was a period of extensive glaciation in Central Africa. The importance of a study of the position of the snow-line on the East African mountains for the explanation of the former climatic regimen is stressed by Flint (1959) in his survey of the available data. A temperature reduction on Mt. Kenya of 5°C and on Kilimanjaro of 7°C may probably be inferred.

This period of lower temperature during the Upper Pleistocene must have diminished the evaporation on the plateaux of East and Southern Africa, and have increased the soil humidity. More surface water was probably available for the vegetation and lakes probably enlarged their area considerably. This encouraged the distribution of rain forest and montane



MAP IV. THE MOST IMPORTANT CHANGES IN VEGETATION DURING THE HYPOTHERMAL PHASE.

forest on the higher ranges and plateaux, and the spread of the woodland into the grassland in so far as the winter temperature did not prevent such migration. The area of the Karoo vegetation certainly diminished because of invasion of grassland. The extent of these move-

ments cannot yet be established as much more data is required from various sites to support this explanation.

The main changes in the vegetation pattern of Africa during this period of lower temperature have been indicated on Map IV. No effort has been made to give a detailed representation as the number of sites which have been studied is still too small. In northern Africa the desert areas have been sketched in those parts which at present have the highest mean July temperature.

The lower temperature affected especially the elevated temperate areas of Africa because of the more widespread occurrence of frost. The mountain ranges, with their wide variety of habitats, must have been refugia for many frost-sensitive plants (Goodwin 1955). Most plant species therefore have been able to survive this climatic oscillation.

The higher humidity had its greatest influence in the arid and semi-arid regions where a small, but consistent, increase in soil humidity and rainfall caused a considerable shift in vegetation over wide areas. This is especially the case in the flat arid regions in the southern and northern part of the continent, where no topographical features limit a widespread migration of plants.

Most obvious is the advance of the Mediterranean vegetation into the desert. This migration has been substantiated by much evidence. The equatorial rain forest must also have gained much area, especially in Uganda and Katanga, where at present many relics still exist. It is very likely that the coastal area of Eastern Africa, with its present-day high temperature, was also covered partly by tropical rain forest. The mountain vegetation had descended to lower levels and may have penetrated into the drier vegetation types over wide areas. Many isolated forest clumps merged under these conditions. On the top of the highest mountains in East Africa the glaciation must have reached a maximum.

The grassland area of Basutoland pushed the semi-arid vegetation far to the south-west and covered the greater part of the Orange Free State and the southern part of the Transvaal. The temperate forests, of which small relics now exist along the south coast of the continent, extended their area to the north-east and merged into the montane forests further north. During this cooler period the Cape vegetation was able to migrate north on the eastern side of the continent along the mountain ranges of the escarpment.

The available botanical evidence here summarized points to a higher humidity in many parts of Africa during approximately the same period. Several chronologies set up for the Quaternary of Africa on geological, palaeontological and archaeological evidence make provision for a number of so-called pluvial periods. This theory can on botanical records be substantiated for one "pluvial" only. We do however not want to use this ambiguous term for this period as pollen data strongly suggest that a more appropriate name should be chosen. The term "pluvial" suggests conditions entirely different from those which prevailed and it would be better to give a name to this period in accordance with its main characteristic, the lower temperature. The name *hypothermal phase* would be much more appropriate and is proposed here for this phase, which was contemporaneous with the Main Phase of the Würm in Europe. We agree with much of the criticism of the pluvial theory, which has, in recent years, been coming from geological quarters (Cook 1957, Flint 1959? Pickering 1958 and Bishop and Posnansky 1960) especially as the theory has been formulated in East Africa on slender evidence, and has been applied with too much enthusiasm for the rest of the continent.

Evidence from periods older than the Upper Pleistocene, such as the distribution of relic vegetation, also points to a cooler and more humid climate than that of to-day, but this supposition cannot yet be supported by pollen analysis. Pollen data from the Post-Pleistocene in Africa are still too scattered to allow any general conclusions for the younger geological periods.

SUMMARY

The difficulties arising from using climatological maps for botanical purposes are discussed. A broad classification of climatic-ecological regions is proposed for the study of Quaternary plant distribution.

Discontinuous distribution and vegetation relics of a number of floras are described as indications of former different conditions. Special attention is paid to the Palaeotropical Flora, the Mediterranean, the Cape, and the Alpine Holarctic Flora, the Montane and Temperate Forests and the Karoo Flora.

The available evidence from fossil pollen is compared. The fossil pollen spectra of the late Upper Pleistocene strongly indicate a decrease in temperature of a few degrees centigrade for the whole of Africa. In most parts of the continent a higher humidity occurred during this cooler period. The influence of this climatic change is discussed for some areas. It is proposed to use the term "hypothermal phase" for this period and to avoid the term "pluvial", as not being appropriate.

The hypothesis of a world-wide lowering in temperature during the Main Phase of the Würm Glacial is supported. At present little fossil pollen evidence is available for younger and older periods in Africa.

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DISCUSSIONS

- Dr. Brain: Does it seem reasonable to Dr. van Zinderen Bakker to associate glacial periods with reduced temperatures and inter-glacials with increased temperatures and so to extend these climatic changes back through the Pleistocene?
- Dr. van Zinderen Bakker: Evidence is inadequate except for the Würm glaciation, but it seems probable that the changes were world wide and of cosmic origin and that similar conditions applied to earlier glaciations.
- Prof. Balinsky: Would not lower temperature automatically result in more humid conditions without necessarily implying increased rainfall? The primary factor would thus be temperature, but the secondary factor which affects vegetation and animal life is precipitation.
- Dr. van Zinderen Bakker: I would not disagree, but suggest that we emphasize temperature rather than rainfall.

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Geographical and ecological
determinants of
distribution patterns ~

The study of animal distribution in southern Africa has not yet reached a stage where much factual material is available for a general treatment of the environmental control of distribution patterns. None the less, the discussion of general problems even at this stage is desirable, if only to attempt to reach some clarity about the nature of the problems confronting us. The purpose of this paper is to discuss four factors which are generally considered to determine distribution patterns, and about which at least some information is available, namely sea barriers, temperature, rainfall and vegetation. To avoid excessive complication, the scope of this paper is limited to a consideration of terrestrial animals only.

Sea Barriers

At present the effect of sea barriers on animal distribution in southern Africa is obvious enough. However, the fact that the coastline of southern Africa dates only from the first half of the Cretaceous (King 1958) should be borne in mind when dealing with the distribution of more ancient groups. Past excesses in palaeogeographical speculation have led to a present diffidence about the question of former continental connections, particularly amongst workers in the northern hemisphere, as was recently shown in the Royal Society's discussion on the southern temperate zone (*Proc. roy. Soc. Lond.*, B, vol. 152, 1960, no. 949). But however risky it may be to indulge in geographical speculation on the basis of animal distribution, workers on distribution should not tend to leave out of account the available information on palaeogeography. A concurrence of stratigraphical, geomorphological and geophysical evidence makes it difficult not to believe that the ancient supercontinent of Gondwanaland was a reality, and it seems that its final disruption was complete by the mid-Cretaceous at the latest (King 1958). The details of the former continental assembly and of its disruption indeed provide a causal explanation of the main features of south temperate biogeography. The temperate flora and the invertebrate fauna of the southern continents show unmistakable affinities, evidently the legacy of the ancient continental continuity. In the invertebrate fauna, affinity is closest between South America and southern Australia/Tasmania (Brink 1960). Southern Africa appears to be lacking in such a strong south temperate element. This characteristic is also shown by the flora (Skottsberg 1960), and can be accounted for when it is seen how intimately South America and Australia were linked in the Gondwanaland complex, both physically and climatically, through Antarctica (King 1958).

Africa, however, became separated from the super-continent while it was in a relatively warmer position than were the southern tips of South America and Australia, Tasmania. The antarctic element in southern Africa is therefore not as conspicuous as it is in the sister continents. Further, it seems that as far as the vertebrates are concerned, Gondwanaland broke up so long ago that the present distribution pattern shows little if any of its influence (Darlington 1957).

Temperature

Despite the relatively poor representation of antarctic elements in southern Africa, the existence of a distinctive non-tropical "South African" fauna (Poynton 1961a) indicates that latitudinal zonal temperature has had a profound influence on distribution in southern Africa. The immense importance of zonal temperature as a determinant of distribution is shown by the fact that the differentiation of the world's fauna as a whole into tropical and non-tropical components follows the zonation of temperature remarkably closely. The 18°C midwinter month surface isotherm is a convenient means of describing the limit of the tropical region not only in southern Africa (Poynton 1961b); in the northern hemisphere the 18°C midwinter month isotherm (as shown in Philips' University Atlas 1958) coincides with the conventional division between the tropical and northern faunal regions (Darlington 1957) in all areas except south-east Asia. It also conforms generally to the conventional lines of demarcation between the Patagonian and Brazilian divisions of South America. In Australia the effect of thermal zonation is difficult to perceive on account of the enormous central desert.

The particular importance of temperature is also shown by its evident ability to determine distribution independently of the habitat pattern. This effect is well shown in the area of Lake St. Lucia, Zululand, where an apparently abrupt and general faunal change (Poynton 1961a) takes place in a region which shows no marked changes in the habitat pattern from north to south. There is a gradual increase in the rainfall from north to south along the Zululand coastal region (Niddrie 1951), but this increase could not in itself be supposed to make conditions less favourable for the tropical fauna. The general conformity between the faunal pattern and the thermal pattern indicates that the faunal pattern is ultimately determined by the thermal pattern. However, it is not easy to see why this faunal change should occur so abruptly in an area showing a very even temperature gradient. Evidently the long period of physiographical stability in south-eastern Africa has permitted the development of a faunal balance which is now controlled by the overall thermal pattern, rather than by any localized factors. With fluctuation of the general thermal pattern in the past, there has presumably been a corresponding shifting of the faunal pattern, and over a long period of time this repeated to and fro movement may have gathered the ranges of the individual species into the present overall pattern of abrupt change.

Whatever the actual *modus operandi* of temperature may be, it does seem that zonal temperature resembles the disposition of land in being a very long-enduring feature which divides faunas on a regional scale. Indeed, the latitudinal zonation of temperature is a geographical feature which must have existed before the continental pattern had taken on its present form. At present, sea barriers on the whole tend to divide longitudinally, and thermal zonation latitudinally, and together these two factors have served to divide the world's fauna into phyletically distinctive regions. The historical endurance and phylogenetic consequences of latitudinal zonal temperature and sea barriers, together with their patterning on a global scale, distinguish these two factors from rainfall and vegetation, which determine rather the local and contemporaneous pattern of the habitats than the general conditions of existence. Zonal temperature and sea barriers may consequently be regarded as being "geographical" factors, in contradistinction to the more "ecological" factors of rainfall and vegetation.

Rainfall

On the whole, rainfall appears to affect distribution indirectly, through its influence on the habitat (Bowen 1933; Poynton, in press). Its influence is most commonly felt through the vegetation pattern. Temperature also has this indirect effect, in addition to its direct effect shown by its apparent ability to determine distribution independently of the habitat pattern. The consequences of freezing provide an obvious example of its indirect effect *via* the habitat. However, in southern Africa the importance of the direct effect far outweighs that of the indirect effect which temperature shares with rainfall: in southern Africa temperature and rainfall determine distribution patterns in essentially different ways. Consequently, the lumping of temperature and rainfall together under the term "climate" is most undesirable because, by doing so, the very fundamental differences between the major effects of these two factors are obscured. Broadly speaking, while temperature and the disposition of land are factors which impose a regional and phyletic pattern on distribution, rainfall and vegetation are factors which impose patterns of adaptive convergence within a faunal region. Ecology, which is more concerned with adaptive convergences and their relation to the habitat pattern, is thus more usually concerned with rainfall and the vegetation pattern than is zoogeography, where interest in taxonomic patterns brings the discontinuity of land surfaces and zonal temperature into particular prominence.

Vegetation

If the above reasoning is valid, large-scale faunal patterning which is determined mainly by the vegetation patterning should be treated with a great deal of caution. Such patterning is well shown in the east to west savanna-rainforest differentiation of the fauna in equatorial Africa. This differentiation raises the question of the zoogeographical significance of the pattern, and particularly whether it is as important to a zoogeographer as is the differentiation between the fauna of East Africa and that of the Cape Province. Taxonomically, the difference between the western forest and eastern savanna faunas across equatorial Africa is apparently no greater than is the difference between the faunas occurring in forest and in grassland in eastern Africa itself. This latter difference is clearly one of ecological importance only, and the larger division across the continent appears taxonomically to be a similar difference, only on a larger areal scale. Thus in zoogeographical terms there appears to be a fundamentally unified fauna in equatorial Africa, the cool highlands excepted (Poynton 1961b).

In contrast, the difference between the fauna of the Cape Province and that of East Africa is taxonomically marked (Poynton 1961a), and is consequently of great zoogeographical importance. Ecologically, however, the north-south differences are on the whole not as marked as the east-west differences, and indeed the complex eastern coastal biome seems to run virtually uninterrupted from East Africa southwards to Pondoland: or at least appeared to do so before the advent of the European settlers. Africa south of the Sahara thus possesses a very marked ecological but poorly marked zoogeographical differentiation from east to west, and a very marked zoogeographical but less marked ecological differentiation from north to south. This dualism in the pattern is evidently due to the differential effect of zonal temperature on the one hand, and the effect of rainfall acting through the vegetation pattern on the other.

Conclusion

It is concluded that the grouping of temperature and rainfall into the single factor "climate" is heuristically valueless and dangerous, and should be avoided. The environmental factors determining distribution seem rather to divide across the term "climate", and separate out into (i) sea barriers and temperature, which are of particular zoogeographical importance

GEOGRAPHICAL AND ECOLOGICAL DETERMINANTS OF DISTRIBUTION PATTERNS

since they have historical and phylogenetic consequences, and (ii) rainfall and vegetation, which determine more the contemporaneous pattern of the biomes, and whose effects are evident more in the adaptive ecological types than in the phyletic constitution of the fauna.

In the extremely diversified environment of southern Africa, where a single species may be restricted in one part of its range by hot arid conditions, and in another part by cool conditions although the rainfall is favourable, precision in considering the effects of the various environmental factors is of prime importance. The general problems of the control of distribution patterns in southern Africa need to be given far more attention than they have been given in the past, for it is only through concerted work that progress can be made in this vastly complex subject.

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DISCUSSION

- Dr. Winterbottom: Ornithologically there is more resemblance between any given vegetation type in the tropical and temperate regions than there is between different types in the same region. The fundamental distinction amongst birds is between forest and non-forest species.
- Dr. Poynton: Is it really easy to differentiate in birds between mere taxonomic differences on the one hand and systematic differences of phylogenetic significance on the other?
- Dr. Winterbottom: No; it is almost impossible.
- Dr. Bigalke: We must be prepared to consider homoiothermal and poikilothermal animals separately as they may differ in their reactions to temperature.
- Mr. Davis: In the Muridae, ecological factors seem to give the best solution of problems of distribution on present knowledge, though it may be possible to fit these into patterns derived from systematics at a later date.
- Mr. Atwell: Has the effect of man—in extirpation especially—as an ecological factor been given sufficient consideration? For instance, the present distribution of the squarelipped rhinoceros might give rise to quite erroneous theories if we did not know the history of it.
- Dr. Poynton: I agree, and think that we should try to reconstruct on the basis of patterns in groups in which the distribution is not much affected by man.

- Dr. McNae:* Dr. Poynton has used the word "ecology" in three different senses, without defining it. He should be more precise in using this term if he is to make his ideas precise.
- Dr. Poynton:* I agree that in speaking to my paper, I have used the word loosely, but I have been defeated by the absence of adequate terminology; I have experienced difficulty in finding words to fit certain concepts, for instance, to describe "sea-barriers - temperature" and "vegetation & rainfall", and would like to invite ideas.
- Dr. McNae:* Arising out Mr. Attwell's question, it has recently been suggested that savanna is a degradation product, induced by man, and not a natural environment. I think that more consideration should be paid to this.
- Dr. Stuckenberg:* It is generally accepted that most of the ungulates probably evolved in savanna country, which is therefore likely to have existed for a considerable time.

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Pleistocene faunas and
the distribution of mammals
in Southern Africa

The late Dr. Austin Roberts's address, "The Old Surviving Types of Mammals in South Africa", given to the South African Association for the Advancement of Science at Windhoek in 1937, appears to me to mark a turning-point in the study of faunal history in Southern Africa. In it he discussed the historical development of the present-day South African fauna as inferred from its distribution, without considering the limited fossil evidence then available. So far as the recent past is concerned, the volume of such evidence has increased enormously in the succeeding quarter-century; when all allowance has been made for possible synonyms, more than two hundred mammalian species can now be listed from deposits belonging to some part of the Pleistocene.

Although there is no continuous local sequence of Pleistocene deposits in South Africa comparable with that at Olduvai Gorge in East Africa, our major fossil assemblages can be arranged in a succession in which some four or five stages can be recognised by changes in the composition of the fauna. In the present state of our knowledge, such stages are best identified by local site names; the proposal made in 1955 to use East African names throughout the continent has proved premature and must perforce be abandoned.

The earliest of our faunal stages, which may be named the *Sterkfontein* stage, is typified by the main deposit at Sterkfontein and by the Limeworks site at Makapansgat; the *Australopithecus* type site at Taung probably also belongs to this stage, though its fauna displays local peculiarities. Although in the past both Taung and Sterkfontein were repeatedly claimed to be older than Pleistocene, it appears at present that they lie somewhat above the lower limit of the Pleistocene as it is now understood. The Swartkrans and Kromdraai deposits, with a number of secondary sites in the same area, represent a stage later than that of Sterkfontein; this may be named the *Swartkrans* stage. Part of the faunal assemblage from the Vaal River Younger Gravels appear to belong to the Swartkrans stage, but much of it apparently belongs to a later stage, best named, from a rich site in the north-eastern O.F.S., the *Cornelia* stage. The assemblage from the Florisbad site near Bloemfontein is in turn unquestionably later than the *Cornelia* stage; the Makapansgat Cave of Hearn's deposit may prove to span the intervening period, although it appears to be mainly equivalent to Florisbad. This *Florisbad* stage may have to be divided into earlier and later phases. A further stage must be interposed between the end of the Florisbad stage and the present day, but this is not yet well characterized, as the available evidence comes from human occupation

	VAAL RIVER DEPOSITS	CAVE DEPOSITS	OPEN SITES
RECENT	"YOUNGER GRAVELS"	NUMEROUS	SITES
?		PEERS CAVE BORDER CAVE	KALKBANK
FLORISBAD STAGE		WONDERWERK MAKAPANGSAT (CAVE OF HEARTHS)	VLAKKRAAL FLORISBAD
CORNELIA STAGE			HOPEFIELD CORNELIA ? ZULULAND COAST
SWARTKRANS STAGE		BOLT'S FARM KROMDRAAI SWARTKRANS STERKFONTein EXT.	? VIRGINIA ? LANGEBAANWEG
STERKFONTein STAGE		MAKAPANGSAT (LIMEWORKS) ? TAUNG STERKFONTein (MAIN SITE)	

Fig. 1. Sequence of recognised pleistocene faunal stages in Southern Africa, with correlation of principal sites.

sites which do not give a comprehensive picture of the fauna; it has therefore no acceptable name at present.

All the type sites and the majority of known secondary sites are concentrated in the inland plateau region. A classic site on the Zululand coast probably belongs to the Cornelia stage; in the south-west Cape there are two important sites, that at Langebaanweg provisionally assigned to the Swartkrans stage, and that near Hopefield to the end of the Cornelia stage.

Recent studies have considerably altered our earlier impression of these faunas. It is now clear that in both the Sterkfontein and the Swartkrans stages extinct species predominate. About 30 per cent of the species recorded in the Sterkfontein stage are at present tentatively identified with living forms, but experience suggests that this estimate will almost certainly prove excessive as the material becomes more completely known. In the Cornelia stage about 50 per cent of the recorded species can be fairly definitely identified as living forms; in the Florisbad stage as a whole living species constitute about 80 per cent, the remaining extinct forms being progressively eliminated during this and the succeeding stage.

Even in the Sterkfontein stage the fauna differs only slightly in general aspect from that of the present. The only truly bizarre or unexpected elements in the Pleistocene faunas are the chalicotheres, the sabre-toothed cats, and perhaps the "three-toed" horses (hipparions); all the other conspicuous extinct species, the baboons and elephants, the hypsodont pigs, the giant giraffes (sivatheres), and the numerous antelopes, are close relatives if not ancestors of existing types.

The species provisionally identified as recent in the Sterkfontein stage include many small mammals, insectivores, bats and rodents; among larger mammals are the two rhinoceroses, the hippopotamus, giraffe, Cape buffalo, eland, kudu, blue wildebeest, and impala. To these may be added in the Swartkrans stage the brown hyaena, lion, Burchell's zebra, red hartebeest, and springbok. Most of these specific identifications may however need to be revised.

In the Cornelia stage, practically all the large recent species tentatively identified in earlier stages can be recognized with much greater confidence; further additions, either definite or tentative, to the list include the Chacma baboon, spotted hyaena, quagga, warthog, black wildebeest, reedbuck, grey duiker, bloubok and sable antelope. In fact, most of the larger species appear to be present at this stage alongside of related extinct forms; the position regarding the small species is not clear, as good cave sites of this stage are lacking. Some larger recent species not at present known before the Florisbad stage, such as the vaal-ribbok and klipspringer, may be absent from deposits of the preceding stage only by chance. The most dramatic new arrival during the Florisbad stage is the African elephant, which fills a place left vacant by the extinction of the elephant species present in the Swartkrans and Cornelia stages.

It is clear that the African elephant must be regarded as an immigrant type, probably derived from west central Africa. Some other recent species which appear for the first time either in the Florisbad or the Cornelia stage may also be immigrants, but others may prove to be descended from allied species present in the Sterkfontein or Swartkrans stages.

The most striking departures from the present-day distribution of existing species are shown by the Hopefield assemblage, belonging to the end of the Cornelia stage; this includes not only the reed-buck, absent from the south-western Cape Province in historic times, but also the blue wildebeest, now essentially tropical; on the other hand, it lacks both the red hartebeest and the grey duiker, present in the same area in historic times, and identified inland during the Cornelia stage. In the inland plateau region there is evidence of a southward extension of both the tsessebe and the lechwe during the Florisbad stage if not already in the Cornelia stage. Isolated relict populations of these once more widely distributed species, or islands of species which have in fact become extinct, might conceivably have persisted into

recent times alongside of existing island or relict types. Although Roberts inferred that recent species limited to a restricted area in southern Africa, such as the mountain zebra and the vaal-ribbok, probably represented in the main an earlier faunal stratum than those with a continuous northward extension, the available fossil evidence does not warrant so simple an interpretation.

Much has been made of possible climatic fluctuations during the Pleistocene as determining factors in faunal change. The available evidence suggests that periods of diminished rainfall, even if of relatively short duration, produced more effect than increases in rainfall, although, as Roberts pointed out, the eastern part of southern Africa must always have remained wetter than the western, and so provided a refuge for types which could not readily adapt themselves to drier conditions. Roberts also justifiably inferred that dry conditions must have extended into the equatorial region at least once and probably more than once, forming a bridge or raft for the passage of species between the arid north-east and the arid south-west of Africa.

The essentially "African" aspect of the fauna of the Sterkfontein stage poses the problem of the origin of the African Pleistocene fauna as a whole. No good Pliocene faunal assemblage has yet been recovered south of the Sahara, so that the Pleistocene and recent faunas of Africa appear like the topmost twigs of trees projecting above the top of a blank wall. There are unquestionable affinities between these African faunas and the Pliocene faunas of Southern Eurasia, but these have frequently been overvalued, fostering the conception that in the later Pliocene or even early Pleistocene Africa was overrun by an Eurasian fauna. The cumulative evidence regarding the earlier Pleistocene faunas of Africa rather indicates that the continent must have been faunally autonomous throughout the Pliocene, and that African mammals migrated outwards into Eurasia both before and during the Pleistocene.

DISCUSSION

Prof. v. Zinderen Bakker: Were there indications of a more tropical fauna than at present at Hopefield? And at Langebaan?

Prof. Wells: The Langebaan evidence is insufficient for generalizations, but the first impressions at Hopefield are that the fauna was of a more tropical type than at present.

Prof. Balinsky: Large mammals have such a wide range of temperature tolerance that they may not be good indicators of climate.

Prof. Wells: That is so; I have had to point this out to my colleagues in Europe in connection with the hippopotamus.

Dr. McNae: Most of the animals to which Prof. Wells refers are browsers rather than grazers. This tends to support my previous suggestion on the artificiality of the savanna.

Dr. Bigalke: Which species does Dr. McNae classify as browsers?

Dr. McNae: Giraffe and Blue Wildebeest.

Dr. Bigalke: I do not agree that the Blue Wildebeest is a browser. Several tropical species, including this wildebeest are known historically from Kuruman and other places in the northern Cape where they do not occur today. But the gap between there and Hopefield is certainly a wide one.

Prof. Wells: They may have come via the east coast.

Dr. Poynton: Many tropical forms have a remarkable tendency to come as far south as the Vaal and to extend along the valley to the northern Cape.

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A preliminary report on
the distribution and
approximate size of
population of some ungulate
mammals in
South West Africa

Modern works on the distribution of Ungulate Mammals in South West Africa are those of Wilhelm (1931), Shortridge (1934) and Bigalke (1958). Older accounts are those of Fischer (1914) and that published by the German Colonial Office in 1913.

The purpose of the present study has been to determine the distribution and approximate sizes of the populations of Kudu, Gemsbok, Springbok, Eland, Hartebeest and Hartmann's Mountain Zebra primarily in the farming areas of the Territory, but including also the distribution in the Bantu Reserves within the border of the Police Zone (Fig. 1).

In view of this limitation I have not attempted to compare my findings with those of Shortridge (1934) and Bigalke (1958), as their field of investigation was more extensive. It is, however, my intention to carry out a complete investigation of the distribution of ungulate mammals in the remaining parts of the Territory and comparisons with previous findings will be included in a later publication.

In the summer of 1960 a game census was undertaken by the Police authorities at the request of the Nature Conservation Section of the Administration of South West Africa. Occupiers of farms were asked to record on questionnaires their estimates of the numbers of each species occurring on their properties. The Chief Bantu Commissioner was responsible for the survey in the Bantu Reserves.

Accurate information on the distribution and a sound idea of the number of each species was obtained as the percentage of return of questionnaires for the farming area was 82 per cent and a complete survey of all the Bantu Reserves was made.

The distribution of the six species was firstly recorded on large scale magisterial district maps on which all the farms and Bantu Reserves are annotated. From these maps a summarized map, to illustrate the distribution, was drawn for each species (Figs. 2-7).

The distribution was correlated with the rainfall zones (Fig. 8, Weather Bureau, 1935), and the vegetation regions (Fig. 9).

I have rejected the estimated numbers for the different species in the Bantu Reserves in view of their probable inaccuracy and only that for the farming area was calculated. The numbers quoted must be regarded as conservative estimates.

The nomenclature used is that of Ellerman, Morrison-Scott and Hayman (1953).

RESULTS OF INVESTIGATION

Kudu *Tragelaphus (Strepsiceros) strepsiceros* (Pallas).

The Kudu is the most widely distributed of all the species considered, occurring between Longitude $13^{\circ} 48'$ and 20° E. and Latitude $18^{\circ} 30'$ and $28^{\circ} 54'$ S. (Fig. 2), although approximately 88.5 per cent of the population is found north of Latitude 24° S. The size of the population on farms is estimated at 60,810.

Kudu occur in the rainfall zones (Fig. 8) which range from 100 mm. to 550 mm. p.a. and in the following vegetation regions (Fig. 9):



Fig. 1. Map of South West Africa showing the Farming Area including the Bantu Reserves.

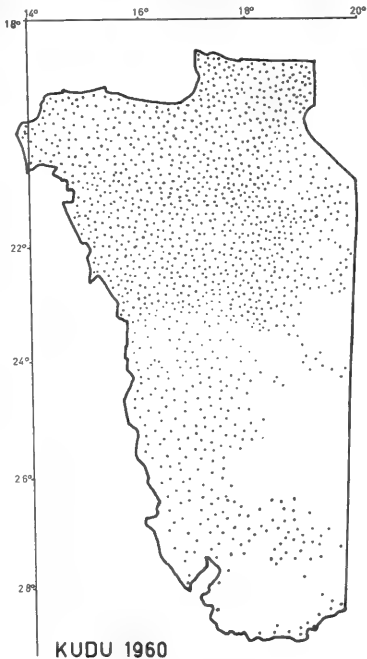


Fig. 2. Map of the Farming Area, including the Bantu Reserves, showing the distribution of Kudu.

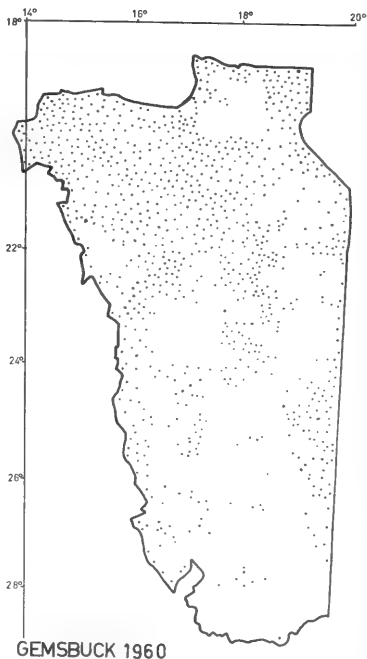


Fig. 3. Map of the Farming Area, including the Bantu Reserves, showing the distribution of Gemsbuck.

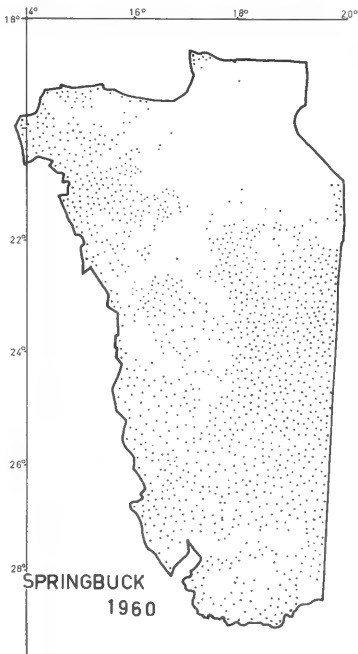


Fig. 4. Map of the Farming Area, including the Bantu Reserves, showing the distribution of Springbuck.

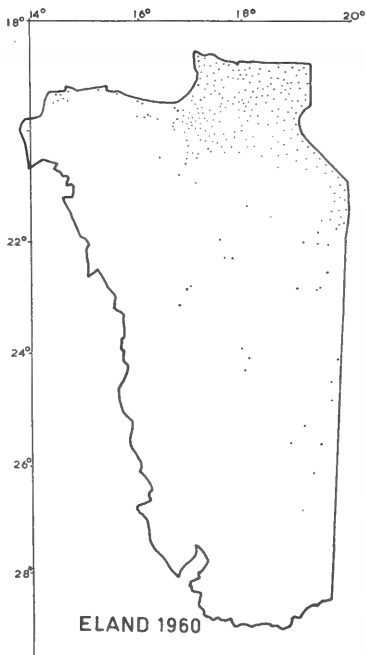


Fig. 5. Map of the Farming Area, including the Bantu Reserves, showing the distribution of Eland.

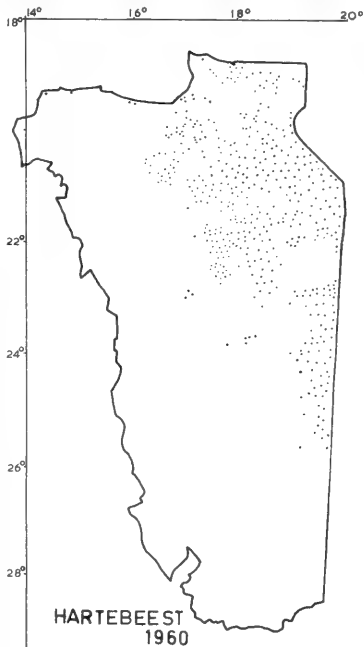


Fig. 6. Map of the Farming Area, including the Bantu Reserves, showing the distribution of Hartbeest.

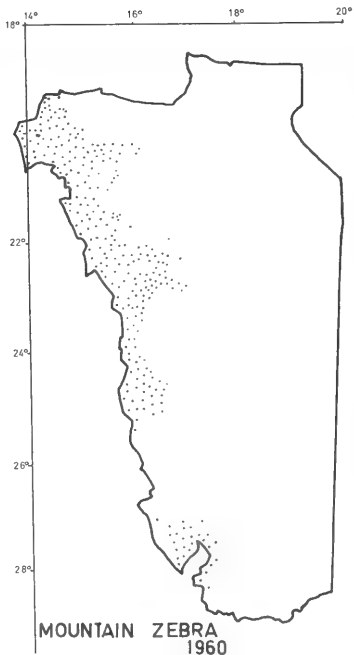


Fig. 7. Map of the Farming Area, including the Bantu Reserves, showing the distribution of Hartmann's Mountain Zebra.

PRELIMINARY REPORT ON DISTRIBUTION AND NUMBER OF S.W.A. UNGULATES

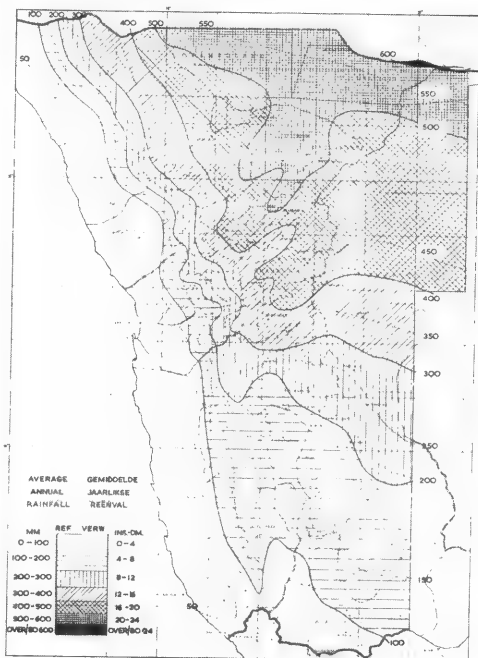


Fig. 8. Rainfall Zones. Reprint from Average Rainfall South West Africa.

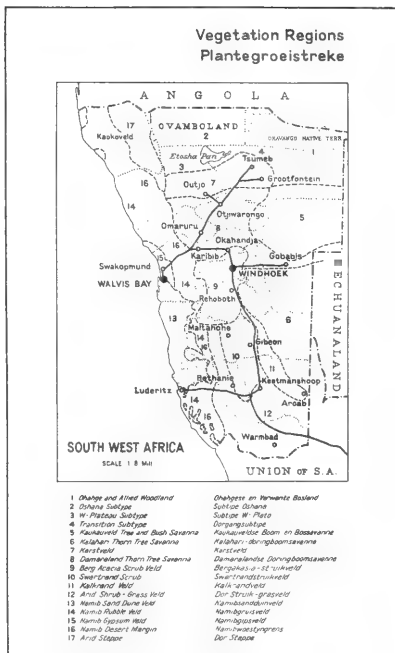


Fig. 9. Vegetation Regions. Reprint from Report of the Long Term Agricultural Commission.

Ohahge and Allied Woodland (1), W-Plateau Subtype (3), Transition Type (4), Kaukaveld Tree and Bush Savanna (5), Kalahari Thorn Tree Savanna (6), Karstveld (7), Damaraland Thorn Tree Savanna (8), Berg Acacia Scrub Veld (9), Swartland Scrub (10), Kalkrand Veld (11), Arid Shrub-Grass Veld (12), Namib Sand Dune Veld (13), Namib Rubble Veld (14) and Namib Desert Margin (16).

Gemsbok *Oryx gazella* (Linnaeus).

The Gemsbok occurs in the same regions as were defined for the Kudu but is less evenly distributed south of Latitude 22° S. (Fig. 3). Approximately 58·2 per cent of the population occurs between Latitude 20° and 24° E. and the size of the population on the farms is estimated at 24,429.

It is found in the rainfall zones ranging from 50 mm. to 550 mm. p.a., and occurs in the same vegetation regions as the Kudu.

Springbok *Antidorcas marsupialis* (Zimmerman).

The Springbok is distributed between the same Longitude and Latitude lines as Kudu and Gemsbok but is practically absent between Longitude 16° and 20° E. and Latitude 18° 30' and 21° S. (Fig. 4). Approximately 73·5 per cent of the population occurs south of Latitude 22° S. and the size of the population on the farms is estimated at 37,280.

It occurs in the same rainfall zones and the same vegetation regions as the Gemsbok, except that it is absent from Ohahge Allied Woodland.

Eland *Taurotragus oryx* (Pallas).

The Eland is distributed mainly between Longitude 16° and 20° E. and Latitude 18° 30' and 22° S. A small number occur in the most north-westerly section of the farming area and also close to the Bechuanaland border. Scattered groups recorded elsewhere in the farming area represent restockings by individual farmers (Fig. 5). The size of the population on the farms is estimated at 6,080.

Eland are largely confined to higher rainfall zones (i.e. 400 mm. to 550 mm. p.a.) than the preceding three species; and this investigation indicates that the natural habitat of Eland is restricted to the following vegetation regions:

Ohahge and Allied Woodland (1), W-Plateau Subtype (3), Transition Subtype (4), Kaukaveld Tree and Bush Savanna (5), Kalahari Thorn Tree Savanna (6) and Karstveld (7).

Hartebeest *Alcelaphus buselaphus* (Pallas).

The Hartebeest is distributed between Longitude 16° and 20° E. and Latitude 19° and 25° 42' S. (Fig. 6). Approximately 50 per cent of the population occurs between Longitude 18° and 20° E. and the total population on the farms is estimated at 6,325.

Hartebeest occur in rainfall zones which range from 200 mm. to 550 mm. p.a. and in the following vegetation regions:

Ohahge and Allied Woodland (1), W-Plateau Subtype (3), Transition Subtype (4), Kaukaveld Tree and Bush Savanna (5), Kalahari Thorn Tree Savanna (6), Karstveld (7) and Damaraland Thorn Tree Savanna (8).

Hartmann's Mountain Zebra *Equus (Hippotigris) zebra hartmannae* Matschie.

This Zebra is distributed between Longitude 13° 48' and 17° 36' E. and Latitude 19° 18' and 28° 24' S. (Fig. 7), with approximately 83·2 per cent of the population occurring north of latitude 24° S. The size of the population on the farms is estimated at 10,520.

It is found in rainfall zones ranging from 50 mm. to 400 mm. p.a. and occurs in the following vegetation regions:

W-Plateau Subtype (3), Karstveld (7), Damaraland Thorn Tree Savanna (8), Namib Sand Dune Veld (13), Namib Rubble Veld (14) and Namib Desert Margin (16).

SUMMARY

The area of investigation has been limited to the whole of the farming area in the Territory as well as to those Bantu Reserves within the border of the Police Zone. The distribution and approximate size of population (for farming area only) of six Ungulates, viz. Kudu, Gemsbok, Springbok, Eland, Hartebeest and Hartmann's Mountain Zebra, has been determined. The distribution has been correlated with Rainfall Zones and Vegetation Regions. This account is an outcome of the Game Census which was held in the summer of 1960.

ACKNOWLEDGEMENTS

I wish to thank the Chief Game Warden, Mr. B. J. G. de la Bat, for his personal interest and valuable criticism; the Police authorities who undertook the Game Census: Mr. D. Moore, (Drawing Office, Survey Dept., Windhoek), who not only supplied me with numerous maps but also undertook the copying of the figures.

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The distribution
of ungulates
in the Orange Free State

This paper is based on information obtained as a result of enquiries published with the assistance of the Regional Manager and District Correspondents of the South African Broadcasting Corporation in the Orange Free State. Their help is gratefully acknowledged.

In making these enquiries, care was taken to distinguish between natural populations of ungulates and animals re-introduced by the farming community. No population was classified as "natural" unless the family giving the information had lived on the farm in question for at least three generations, and could thus testify that it did not stem from recent introductions. Using this fairly strict criterion, I was surprised to find how much is still left in the Orange Free State at the present time, despite short-sighted farming practices and widespread poaching by all races.

NATURAL POPULATIONS

Steenbok

This small buck is fairly generally distributed throughout the Province, but occurs in greatest numbers (i.e. averaging 20 or more per farm per district) along rivers and in the mountainous country of the Eastern Free State (Fouriesburg, Tweeling, Petrus Steyn, Boshoff, Theunissen, Brandfort, Hoopstad, Koffiefontein).

Duiker

This species occurs naturally in the central and western Free State in numbers which average 25 per farm (Kestell, Brandfort, Theunissen, Boshoff, Koffiefontein, Smithfield, Bethulie).

Vaal Ribbok — Rooi Ribbok

These animals are recorded from Fouriesburg, Tweeling, Harrismith, Theunissen, Koffiefontein, Bethulie, Ficksburg, Smithfield and Zastron.

A remarkable assertion made by 60 per cent of the farmers concerned is that, where both species occur together, the Rooi Ribbok is diminishing in numbers, despite protection. The reason given for this is that Vaal Ribbok males are prone to attack herds of the Rooi

Ribbok and even to kill individuals. I myself witnessed a fight between males of the two species and saw the vanquished Rooi Ribbok badly wounded and put to flight by the Vaal Ribbok.

Klipspringer

This species is now very rare. A few are seen regularly in the Fouriesburg, Zastron and Kestell districts.

Blesbok

These animals are found throughout the Free State, the largest concentrations occurring in the northern and north-eastern parts of the Province. Some of the surviving herds number 50 animals or more, and a conservative estimate puts the total population of the Province at about 12,000.

Springbok

Large herds of 200 or more are found in the western, south-western and central Free State, and the total population in the Province must be well in excess of 10,000.

Black Wildebeest

Only a few natural herds are left, and from these animals are sold to farmers for restocking. Unfortunately, however, during the last two years, animals have also been sold to dealers who exported them, and thus these animals were lost to our country. Amongst those that remain, herds of over 50 occur in the Odendaalsrus, Kroonstad, Harrismith and Dewetsdorp districts, and two smaller herds exist in the Bloemfontein and Hoopstad districts.

GAME RESERVES

In general, the ungulates occurring in Free State game reserves are not natural populations. Much good work has been done in the restocking of these reserves with many different species. Unfortunately, however, enthusiasm for restocking has sometimes been carried too far, even to the point of introducing animals which are foreign to the country, as at the Franklin Game Reserve in Bloemfontein, where Fallow Deer have been introduced and plans were made to bring in Barbary Sheep as well.

The most important of the Free State reserves is undoubtedly the Willem Pretorius Reserve near Allemanskraal. Here there are herds of Red Hartebeest, Eland and Black Wildebeest, which may become important sources of animals for restocking farms. In the Franklin Game Reserve only a herd of Eland is likely to acquire similar importance and that only if measures are taken against inbreeding.

INTRODUCTION AND RE-INTRODUCTION OF ANIMALS ON PRIVATE FARMS

Reviewing activities in this direction, especially during the last ten years, we may be grateful for what has been achieved by private farmers in restocking their land with Springbok, Blesbok, Eland, Black Wildebeest and different types of small buck. All of these are now found in several districts where natural populations have disappeared. At the same time, restocking has again often been carried to unwise extremes and farmers eager to encourage

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large game animals have introduced species unsuited to the area, and even totally foreign types, such as Fallow Deer, Dromedary, Water Buffalo, Nylgai, Barbary Sheep, Hog Deer and Llamas.

Amongst indigenous forms which have been re-introduced into denuded areas are the Steenbok, Duiker, Klipspringer, Springbok, Blesbok, Black Wildebeest, and Vaal and Rooi Ribbok. Other introductions of which there are no natural populations include Blue Wildebeest, Red Hartbeest, Eland, Impala, Gemsbok, Lechwe, Reedbuck, Bushbuck and Giraffe.

This somewhat haphazard restocking programme has had some disastrous results. In some instances, there was an undesirable mixing of species with resultant crossbreeding, as in the case of the Black and Blue Wildebeest on farms in the Harrismith district. Crossbred animals may now be seen in the Johannesburg Zoo. More distressing was the mortality which sometimes occurred. Of the Gemsbok introduced by farmers, nearly 90 per cent died, and the remainder are not doing at all well. In areas with sufficient bush Impala fared satisfactorily, but amongst Lechwe, Reedbuck and Giraffe the casualties were very high, amounting on many farms to 100 per cent of the animals introduced.

To my mind, the blame for this situation must not rest entirely with the farmer, who is trying to encourage and conserve game animals, but with the fact that there is no Nature Conservation Department to advise them of the suitability or otherwise of the animals they propose to introduce. However, the outlook for the future is still a good one, and we may well be encouraged to find that there are so many farmers who wish to restock their land, not for the purpose of shooting, but for the love of seeing these animals on their farms.

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Distribution patterns of
Southern African Muridae,
with notes on some of their
fossil antecedents

INTRODUCTION

In this preliminary attempt to define faunal areas on the basis of the distribution patterns of the species of Muridae occurring in Southern Africa, the problem has been approached with the Aethiopian Geographical Region as background and with the simplest classification of biotic zones based on the major vegetation types as a starting point. The murids of Southern Africa (south of the Kunene-Zambezi) show varying degrees of attachment to the biotic zones Savanna, South West Arid and South-West Cape (Fig. 1). A consideration of their distribution within these zones brings to light a degree of correspondence sufficiently close to give reality to the approach made here of taking vegetation types as a starting point. Subdivisions of the zones, especially of the diversified Savanna zone, on the basis of murid distribution gives even more support for regarding vegetation as the most meaningful ecological summary of the influences of soil, climate, topography and other static and dynamic environmental factors.

BIOTIC SUBDIVISIONS OF THE AETHIOPIAN GEOGRAPHICAL REGION

Sclater (1896) divided the Aethiopian Region into four: The Saharan, West African, Cape and Malagasy subregions. In recent years the Malagasy subregion has been given regional status (Darlington 1957). The Aethiopian Region may thus be defined as continental Africa south of the Sahara. Sclater's Cape subregion extended to the fringes of the Congo Basin in the north-west and to the Tana watershed (just north of the equator) in the north-east where it graded into the Saharan subregion. That there is some significance in this meeting point (here termed the Sclater line) of his two subregions will become apparent below (see p. 62). Chapin (1923, 1932) worked out avifaunal subdivisions largely on the basis of vegetation types which he found best fitted the distribution of birds. His West African subregion and East and South African subregion correspond essentially to those of Sclater's — understandably, since both are based on the broad separation of tropical forest from savanna and desert.

The map reproduced here (Fig. 1) is based on that of Moreau (1952) which is a simplification of Chapin's map, but with Moreau's addition of the south-western Cape winter

rainfall (Cape macchia) as a distinct biotic subregion. The boundaries of the vegetation zones in Fig. 1 are slightly modified from Moreau to conform with the recently published vegetation map of Africa south of the tropic of Cancer (Keay 1959) but the names used by Moreau for the subregions are retained.

SOUTHERN AFRICA AS A FAUNAL AREA

The northern boundary

As can be seen from Fig. 1 the South West Arid lies to the south of the Kunene-Zambezi boundary with the important exception that there is a tongue along the west coast, penetrating into southern Angola across the Kunene River. South West Arid mammals penetrate to 12° S. (Hill and Carter 1941) and this point also coincides with the northern limit of the biotic zone as delimited on the basis of vegetation. Koch (1958) for example has shown that the Kunene River in itself is no barrier to the Tenebrionidae and that the subdivision extends certainly to 15° S. and probably to 12° S. The Kunene River turns northwards in longitude 15° E. and from that point the boundary follows international borders to the Zambezi at Katima Mulilo, Caprivi Strip. There is thus no natural barrier until the Zambezi is reached. This stretch of country however, is a transition belt between the South West Arid and the Savanna zone and in this sense has some meaning faunistically.

The biotic zones in Southern Africa

The South-West Cape.—The South-West Cape is distinct climatically and biotically. The south-western portion has a strictly Mediterranean climate with winter rainfall. Towards the east, along the coast as far as Port Elizabeth, annual rainfall becomes more and more regularly distributed throughout the year. The zone is cut off from the Karoo section of the South West Arid by the northern limit of the Folded Belt; from the Savanna by the George-Knysna forests and from the southern Namib by the transition to the Cape macchia. The zone as delineated on the map (Fig. 1) corresponds to the Cape macchia.

The South West Arid.—The South West Arid lies in the under 20 inch rainfall area and consists of true desert (the Namib) and semi-desert (Kalahari and Karoo). It is divided across the middle by the Orange River and contains within it the western and southern portions of the Great Escarpment. It extends across the Kunene to about latitude 12° S.

Southern Savanna.—After sweeping across the subcontinent the Southern Savanna occupies the eastern part of Southern Africa and continues down the east coast to meet the South-West Cape. It contains the rest of the Great Escarpment running northwards to the Zambezi River with its montane grasslands and forest patches, as well as the highveld grasslands and the bush—and lowveld woodlands and the low-lying tropical Mozambique Plain.

Forest. Isolated patches of montane and subtropical evergreen forest are distributed in the Savanna zone and in the South-West Cape, mainly below the Great Escarpment from Southern Rhodesia to the Cape. Endemic species of mammals are extremely few in number. No species of Muridae is a true forest form. There are thus no ecological equivalents in Southern Africa to such species that Ansell (1960) lists either as encroaching marginally into Northern Rhodesia from Lowland Forest or as having a relict distribution outside their main distribution area in the Lowland Forest.

ENDEMISM AND DISTRIBUTION PATTERNS OF THE MURIDAE

Roberts (1937: 1951, p., xxii-xxiv) went into the question of endemism, of ancient and modern genera and of the significance of their ranges. His analysis of distribution is in somewhat general terms and since he published no distribution maps it is difficult to arrive at a classification of distribution patterns from his book. Now that detailed maps have been

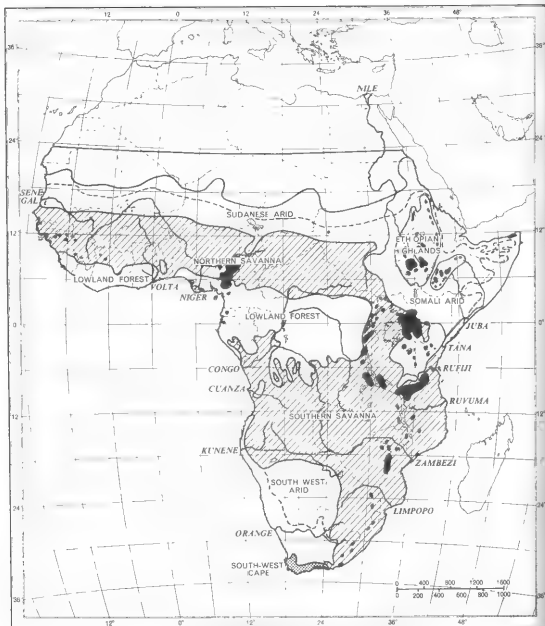


Fig. 1. The main biotics zones of Africa south of the Sahara. Montane forest in black. (After Moreau 1952 and Keay 1959).

compiled it is instructive and revealing to approach the problem of making subdivisions of the biotic zones of Southern Africa from the point of departure taken by Ansell (1960) and to make a preliminary classification of the distribution patterns of the Muridae on the basis of endemism, marginal encroachment and relict populations. It must be borne in mind that the taxonomic status of the species mapped here is in some cases still uncertain and that the distribution records for many are incomplete, especially those which extend beyond Southern Africa.

Ansell (1960) classifies the 191 species of mammals amongst which he recognises 36 species of indigenous Muridae found in Northern Rhodesia according to their distribution patterns using Chapin's two main faunal subdivisions as a framework. He points out that Northern Rhodesian species typical of the West African subregion (Lowland Forest of Fig. 1) have two patterns: the one a relict pattern, with discontinuities determined by the existence in the past of more extensive forest during one or other of the Pleistocene Pluvials and the other a marginal encroachment from the Lowland Forest block. The savanna species of his East and South African subregion (Northern and Southern Savanna of Fig. 1, which extends across the continent below the Sahara to West Africa) either extend throughout the subregion, with some reaching the Palaearctic or have a restricted distribution within it, sometimes continuous, sometimes discontinuous. Other species are grouped as occurring throughout the Region, a few of which extend into the Palaearctic.

The categories employed by Ansell (1960) to classify the ranges of Northern Rhodesian mammals, i.e. as endemic, marginal or relict, have here been applied to the species of Muridae occurring in Southern Africa.

SPECIES-ASSEMBLAGES OF THE BIOTIC ZONES

The South-West Cape (Table 1). There are three species of Muridae which are endemic to the South-West Cape viz. *Praomys verreauxi*, *Acomys subspinosus* and *Tatera afra*. The following species are represented by fairly distinct subspecies or isolated relict populations: *Dasyms incommis* (ssp. *capensis*), *Saccostomus campestris*, *Steatomys* sp., *Otomys laminatus* (ssp. *silbhaueri*), *O. saundersiae* (ssp. *karovensis*) and *Mystromys albicaudatus*. All but *S. campestris* are Savanna species, one of which, *D. incommis*, extends throughout the Southern and Northern Savanna to West Africa. The remaining species may be classified as encroaching on the South-West Cape from their main distribution area without marked discontinuities in distribution.

South West Arid (Table 2). There are ten species which are either confined to the South West Arid or range only slightly outside it: *Zelotomys woosnami*, *Aethomys granti*, *Petromyscus collinus*, *Malacothrix typica*, *Otomys unisulcatus*, *Parotomys brantsi*, *P. littledalei*, *Desmodillus auricularis*, *Gerbillus pacha* and *G. vullinus*. All but *M. typica*, *O. unisulcatus*, *P. brantsi*, *D. auricularis* and *G. pacha* are strictly confined to the subregion. Species with isolated relict populations of subspecies status are: *O. irroratus* (ssp. *coenosus* at Kuruman and an isolated population in the Upper Karoo), *O. sloggetti* (ssp. *sloggetti*), *Tatera brantsi* (ssp. *namaquensis* on lower Orange River and ssp. *miliaria* in the Upper Karoo). The other species have substantial ranges in this and the Savanna zone.

Almost every one of the species found in the South West Arid has a different pattern within the subregion. The subdivision of the South West Arid on the basis of the distribution patterns of the Muridae would divide it at least into the following sub-zones: northern (e.g. *P. littledalei* ssp. *namibensis*), and southern Namib; the western Escarpment and associated upland mountain blocks (*P. collinus*); the Kalahari basin (*T. b. perpallida*, *T. l. schinzi*, *Z. woosnami*) and the Karoo (*A. granti* and *O. unisulcatus*).

TABLE 1
DISTRIBUTION STATUS OF MURIDAE OCCURRING IN THE SOUTH-WEST CAPE
BIOTIC ZONE

<i>Endemic</i>	<i>Relict*</i>	<i>Marginal</i>
1. <i>Praomys verreauxi</i>
2.	<i>Praomys natalensis</i>
3.	<i>Dasomys incommisus</i>
4.	<i>Aethomys namaquensis</i>
5.	<i>Rhabdomys pumilio</i>
6.	<i>Mus minutoides</i>
7. <i>Acomys subspinosus</i>
8.	<i>Saccostomus campestris</i>
9.	<i>Steatomys</i> sp.
10.	<i>Dendromus mesomelas</i>
11.	<i>Dendromus melanotis</i>
12.	<i>Malacothrix typica</i>
13.	<i>Otomys laminatus</i>
14.	<i>Otomys irroratus</i>
15.	<i>Otomys saundersiae</i>
16.	<i>Otomys unisulcatus</i>
17.	<i>Parotomys brantsi</i>
18.	<i>Mystrumys albicaudatus</i>
19.	<i>Desmodillus auricularis</i>
20.	<i>Gerbillus paebe</i>
21. <i>Tatera afra</i>

*Species with isolated subspecies or populations whose main distribution is elsewhere.

TABLE 2
DISTRIBUTION STATUS OF MURIDAE OCCURRING IN THE SOUTH WEST ARID
BIOTIC ZONE

<i>Endemic (A)</i>	<i>Near-endemic (B)*</i>	<i>Relict</i>	<i>Marginal†</i>
1.	<i>Thallomys paeudulus</i> ‡
2. <i>Zelotomys woosnami</i> (A)
3.	<i>Aethomys chrysophilus</i> ‡
4.	<i>Praomys natalensis</i>
5.	<i>Aethomys namaquensis</i>
6. <i>Aethomys granti</i> (A)
7.	<i>Rhabdomys pumilio</i>
8.	<i>Mus minutoides</i>
9.	<i>Lemniscomys griselda</i> ‡
10.	<i>Saccostomus campestris</i> ‡
11. <i>Petromyscus collinus</i> (A)
12.	<i>Steatomys</i> spp.
13.	<i>Dendromus melanotis</i>
14. <i>Malacothrix typica</i> (B)
15.	<i>Otomys irroratus</i>
16. <i>Otomys unisulcatus</i> (B)
17.	<i>Otomys sloggetti</i>
18. <i>Parotomys brantsi</i> (B)
19. <i>Parotomys littledalei</i> (A)
20. <i>Desmodillus auricularis</i> (B)
21. <i>Gerbillus paebe</i> (B)
22. <i>Gerbillus vullinus</i> (A)
23.	<i>Tatera brantsi</i> ‡
24.	<i>Tatera leucogaster</i>

*Near-endemic (B), in this table, means limited marginal encroachment into either South-West Cape and/or Savanna.

†Marginal here used in a very broad sense to list Savanna species, most of which have substantial ranges in the South West Arid.

‡Species encroaching marginally, but also with isolated relict subspecies or populations.

Savanna species (Table 3).—The Savanna zone is much more diversified and extensive than the South West Arid and South-West Cape and it is not surprising therefore that there are few species that can be said to be strictly endemic. *Thamnomys dolichurus* is a Savanna endemic but it is, to some extent, dependent upon the proximity of forest. Those Savanna forms that do not penetrate the South West Arid, but reach the South-West Cape along the coast (e.g. *Dasymys incommisus*, *O. laminatus*, *O. irroratus*, *O. saundersiae* and *M. albicaudatus*) form one group. Those that range fairly extensively in the South West Arid, but which are primarily Savanna forms are: *T. paedulcus*, *A. chrysophilus*, *A. namaquensis*, *R. pumilio*, *M. minutoides*, *L. griselda*, *S. campestris*, *O. sloggetti* and *T. leucogaster*. A further group are those Savanna species whose ranges terminate higher up in the Savanna belt e.g. *Cricetomys gambianus* (relict populations in northern Transvaal and Mozambique) and *Pelomys fallax*.

TABLE 3
DISTRIBUTION STATUS OF MURIDAE OCCURRING IN THE SAVANNA BIOTIC ZONE

Endemic (A) Near-endemic (B)*	Relict	Marginal
1. <i>Thamnomys dolichurus</i> (A)
2. <i>Aethomys chrysophilus</i> (B)
3. <i>Thallomys paedulcus</i> (B)
4. <i>Praomys natalensis</i> (B)
5. <i>Aethomys namaquensis</i> (B)
6. <i>Rhabdomys pumilio</i> (B)
7. <i>Mus minutoides</i> (B)
8. <i>Dasymys incommisus</i> (B)
9. <i>Pelomys fallax</i> (A)
10. <i>Lemniscomys griselda</i> (B)
11. <i>Acomys</i> spp. (A)
12. <i>Saccostomus campestris</i> (B)
13. <i>Cricetomys gambianus</i> (A)
14. <i>Steatomys</i> spp. (B)
15. <i>Dendromus mesomelas</i> (B)
16. <i>D. mystacalis</i> (A)
17. <i>D. melanotis</i> (B)
18. <i>D. nyikae</i> (A)
19.	<i>Malacothrix typica</i>
20. <i>Otomys laminatus</i> (B)
21. <i>Otomys irroratus</i> (B)
22. <i>Otomys angoniensis</i> (A)
23. <i>Otomys saundersiae</i> (B)
24. <i>Otomys sloggetti</i> (B)
25. <i>Mystromys albicaudatus</i> (B)
26.	<i>Desmodillus auricularis</i>
27.	<i>Gerbillus paebe</i>
28. <i>Tatera inclusa</i> (A)
29. <i>Tatera brantsi</i> (B)
30. <i>Tatera leucogaster</i> (B)

*Near-endemic in this table means a fairly substantial hold either in South West Arid and/or South-West Cape.

NOTES ON THE DISTRIBUTION PATTERNS AND HABITAT PREFERENCES OF THE MURIDAE

Subfamily Murinae

1. *Thamnomys dolichurus* (Fig. 5, Map 23; Table 3): Confined to Savanna woodland and extending through the Southern and Northern Savanna to West Africa; dependent upon thickets and forest margins. Funnels down south-east coastal belt to Uitenhage district.

2. *Aethomys chrysophilus* (Fig. 7, Map 31; Tables 2, 3): A Savanna woodland species occurring in Southern Savanna to Kenya (Sclater line). Distribution pattern defines transition from grassland to woodland in Natal and Transvaal. Relict population in South West Arid around Kuruman and marginal from Savanna zone into north-western Kalahari.

3. *Thallomys paedulus* (Fig. 7, Map 34; Tables 2, 3): From Orange River northwards through South West Arid and Southern Savanna to equator (Sclater line). Dependent upon camelthorn and other *Acacia* groves in South West Arid (*nigricauda* group of 'subspecies') and on woodland in bushveld of Natal and Transvaal and Rhodesia (*paedulus* group of 'subspecies'). On the lower Orange River, with its riverine vegetation a southern limit, is an isolated ssp. *shortridgei* of the *nigricauda* group of ssp.

4. *Zelotomys woosnami* (Fig. 2, Map 6 (A); Table 2): Strictly endemic to South West Arid and restricted to Kalahari. Rare, on verge of extinction (?). Replaced by *Z. hildegardae* in Southern Savanna to Kenya and north-eastern Congo.

5. *Praomys natalensis* (Fig. 5, Map 22; Table 1, 2, 3): Throughout Southern and Northern Savanna, also occurring in the Palaearctic (Morocco). Marginal in South West Arid from Savanna zone, not south of Lower Orange River, and not in desert or near desert. Disappears where the south-east coastal Savanna meets South-West Cape zone. Found equally in Savanna woodlands and grasslands. Semi-domestic and present distribution possibly dependent on having followed early human population movements.

6. *Praomys verreauxi* (Fig. 4, Map 14; Table 1): Endemic to South-West Cape. Nearest related forms in (?) Angola (*angolensis*), East Africa (*fumatus*) and West Africa (*daltoni*).

7. *Aethomys namaquensis* (Fig. 6, Map 27; Tables 1, 2, 3): Distributed throughout Southern Africa, but has crossed Zambezi into Northern Rhodesia and Nyasaland, and extends into south-western Angola. Lives amongst rocks, in hollow trees or under bark, in aloes or where none of these is available constructs its own haystack shelters (e.g. in parts of the Kalahari).

8. *Aethomys granti* (Map 7; Table 2): Confined to the Karoo. Very closely related to *A. namaquensis*; overlaps with *A. n. centralis*.

9. *Rhabdomys pumilio* (Fig. 6, Map 28; Tables 1, 2, 3): Generally distributed throughout Southern Africa except in certain tropical savanna woodlands. Western semi-desert forms long-tailed; eastern forms short-tailed. Discontinuously distributed north of the Limpopo in montane grasslands to East Africa (Sclater line). Replaces *L. griselda* (see 13) in Zululand and the eastern Transvaal lowveld.

10. *Mus minutoides* (Fig. 6, Map 26; Tables 1, 2, 3): Generally distributed throughout Southern Africa and northwards in Savanna to West Africa.

11. *Dasymys incommis* (Fig. 5, Map 21; Tables 1, 3): Typical of Savanna and montane areas in Savanna zone to West Africa with a relict ssp. *capensis* in South-West Cape. A swamp rat which appears to be losing its hold in Southern Africa. Funnels down the south-east coast, but still persists at isolated points in Transvaal bushveld and eastern highveld grasslands.

12. *Pelomys fallax* (Fig. 7, Map 36; Table 3): Southern Savanna to East Africa (Sclater line) from north of the Limpopo dry belt. A swamp rat with rather similar habitat requirements to *Dasymys incommis*.

13. *Lemniscomys griselda* (Fig. 7, Map 32; Tables 2, 3): Typically a species occurring throughout Savanna woodlands to East Africa (Sclater line), which seems to be disappearing from the central Kalahari, but co-distributed with *A. chrysophilus* in the north-west. Funnels down the east coast to southern Natal, much as *A. chrysophilus*.

14. *Acomys* spp. (Fig. 4, Map 15; Tables 1, 3): *A. subspinosus* is confined to South-West Cape. The genus *Acomys* is distributed in the Savanna belt northwards from the northern Transvaal and Mozambique to North Africa and eastwards to Pakistan. Its distribution is somewhat discontinuous, especially in the southern part of its range. Attached to rocky situations.

15. *Saccostomus campestris* (Fig. 6, Map 25; Tables 1, 2, 3): South West Arid and Southern Savanna to Kenya and northern Uganda (somewhat north of Sclater line). In the Southern Savanna of the Transvaal and Natal its distribution pattern clearly reflects its attachment to woodland savanna as against grassland savanna. There are relict populations in the Karoo and in the South-West Cape. (One record from Robertson see Davis 1959, p. 147).

16. *Cricetomys gambianus* (Fig. 7, Map 35; Table 3): Southern and Northern Savanna to West Africa. A Savanna species dependent to some extent on forest fringes. In the Zoutpansberg its sporadic occurrence suggests earlier more extensive forest. In Southern Africa it is represented by a relict ssp. *haagneri* in northern Transvaal (Zoutpansberg and Woodbush) and by other ssp. in Mozambique and Southern Rhodesia (Mt. Selinda).

Subfamily Dendromurinae

17. *Petromyscus collinus* (Fig. 2, Map 5; Table 2): Endemic to South West Arid and restricted to the mountain belt fringing the Namib and relict in the Karoo. Lives in rock crevices.

18. *Steatomys* spp. (Fig. 6, Map 29; Tables 1, 2, 3): (at least three species are suspected, but their identity has not been worked out). The genus *Steatomys* appears to be a Savanna form extending to West Africa. In Southern Africa there is a relict form *pentonyx* in the South-West Cape. The genus encroaches marginally from the Savanna into the north-western South West Arid (cf. *A. chrysophilus* and *L. griselda*).

19. *Dendromus mesomelas* (Fig. 5, Map 20; Tables 1, 3): Southern Savanna woodlands to East Africa (roughly to Sclater line) and funnels down the south-east coast to the South-West Cape.

20. *Dendromus mystacalis* (Fig. 5, Map 24; Table 3): Southern Savanna woodlands to East Africa. Funnels down south-east coast to Transkei. Distribution pattern essentially the same as *D. mesomelas* except that it does not occur in the South-West Cape.

21. *Dendromus melanotis* (Fig. 5, Map 19; Table 1, 3): Southern Savanna grasslands, or grasslands in woodland areas to Congo and East Africa (Sclater line). Funnels down the east coast with an isolated relict ssp. *capensis* in the South-West Cape. Encroaches along the Molopo River bed into South West Arid. More of a grassland species than *D. mesomelas* and *D. mystacalis* but with a similar distribution pattern. (The status of the species is in considerable doubt and some of the records may be based on the longer-tailed *D. nyikae* (see 22)).

22. *Dendromus nyikae* (No Map; Table 3): A rare Savanna woodland species represented by forms in the Transvaal lowveld, Nyasaland, Northern Rhodesia and Angola possibly in West Africa (Mt. Nimba, Ivory Coast; Heim de Balsac and Lamotte 1958).

23. *Malacothrix typica* (Fig. 2, Map 3; Tables 1, 2, 3): Primarily a South West Arid species encroaching marginally into Savanna grasslands (highveld) and into the northern fringe of the South-West Cape.

Subfamily Otomyinae

24. *Otomys laminatus* (Fig. 4, Map 17; Tables 1, 3): Savanna grasslands, sub-montane and coastal, funnelling down to South-West Cape where there is an isolated ssp. *silbibauii*. Not known north of latitude 23° S. Distribution markedly discontinuous, possibly dying out.

25. *Otomys irroratus* (Fig. 6, Map 30; Tables 1, 2, 3): Southern Savanna highveld, coastal and montane and sub-montane grasslands, continuously distributed to South-West Cape. Isolated on the eastern Escarpment in S. Rhodesia and not occurring north of the Zambezi unless the related *tropicalis* proves to be conspecific. Relict ssp. *coenosus* around Kuruman, and an isolated population in the Karoo within the South West Arid. An example of persistence in 'oases'.

26. *Otomys angoniensis* (Fig. 7, Map 33; Table 3): Southern Savanna woodlands and grasslands to Angola and East Africa. Often confused with *O. irroratus* and *O. tropicalis* and co-exists with them in some areas. Two ssp. groups in Southern Africa: ssp. group *tugelensis* in Natal, Transvaal and extreme northwest Cape; also Mozambique and S. Rhodesia and ssp. *maximus* group in Okavango and south-western Angola (and Elisabethville *fide* Misonne pers. comm.). Distinguished from *irroratus* s.l. by the absence of a clear round posterior petro-tympanic foramen into the bulla and other dental and skull characters. In South Africa e.g. in Transvaal, has a preference for a drier habitat than *irroratus* where the two are found together.

27. *Otomys saundersiae* (Fig. 4, Map 16; Tables 1, 3): South-West Cape relict ssp. *karoensis*; ssp. *saundersiae* in eastern Cape Savanna, north to the Orange River. Sharing morphological characters and habitat preferences with *O. irroratus* and *O. sloggetti*.

28. *Otomys unisulcatus* (Fig. 3, Map 9; Tables 1, 2): South West Arid and marginal encroachment thence into South-West Cape. Confined to the Karoo south of the Orange River except where it has crossed at one point to Luckhoff, O.F.S. Builds large stick shelters in dry watercourses and feeds on Karoo succulents. Occurs throughout the Noorsveld (which is the bulge into the Karoo of the Savanna zone at its junction with the Cape macchia (Fig. 1)) and reaches the coast in Port Elizabeth region. This suggests that the Noorsveld is biotically South West Arid rather than Savanna.

29. *Otomys sloggetti* (Fig. 3, Map 10; Tables 2, 3): Highveld and montane grasslands of Southern Savanna south of latitude 27° S. Highly subspeciated. Distinct ssp. *sloggetti* in Karoo, ssp. *jeppesi* in eastern Cape, ssp. *robertsi* tops of Basutoland Mountains, ssp. *turneri* north-eastern O.F.S. and extreme south-eastern Transvaal and ssp. *basuticus* lower altitudes in south-western Basutoland. Also known on spur of Drakensberg (Thabathlope, Natal). Selects rocky habitats.

30. *Parotomys brantsi* (Fig. 3, Map 8; Tables 1, 2): Typical of the South West Arid, occurring throughout the Karoo and extending north of the Orange River up beds of Molopo and Nossob rivers. Marginal encroachment into South-West Cape from the north. Apparently not north of the lower reaches of the Orange River.

31. *Parotomys littledalei* (Fig. 2, Map 4; Table 2): Confined to South West Arid, occurring in the Karoo and Namaqualand with an isolated ssp. *namibensis* in the northern Namib. An example of a discontinuity between northern and southern Namib at Swakopmund. Has a range wider than *P. brantsi* and rather similar burrowing habits but is relatively less numerous where the two species co-exist.

Subfamily Cricetinae

32. *Myxomys albicaudatus* (Fig. 4, Map 16; Tables 1, 3): A Savanna species of highveld and montane grasslands not known north of latitude 26° S., with an isolated population in the South-West Cape. Widely distributed but local in occurrence. An indicator of the boundary between Savanna grasslands and woodlands. Remarkably uniform in size and colour for such a widely distributed species.

Subfamily Gerbillinae

33. *Desmodillus auricularis* (Fig. 2, Map 1; Tables 1, 2, 3): Distributed throughout the South West Arid, marginal in the South-West Cape. Main distribution area ends abruptly on South West Arid Savanna border apart from isolated populations in grassland Savanna of western Transvaal, north-western and south-eastern Orange Free State.

34. *Gerbillus paeba* (Fig. 2, Map; Tables 1, 2, 3): Throughout the South West Arid and much of South-West Cape. Isolated ssp. *exilis* in eastern Cape coastal dunes and ssp. *coombesi* north of the Zoutpansberg in Savanna zone. Distribution pattern suggestive of a wider past

DISTRIBUTION OF SOUTHERN AFRICAN MURIDAE; NOTES ON THEIR FOSSIL ANTECEDENTS

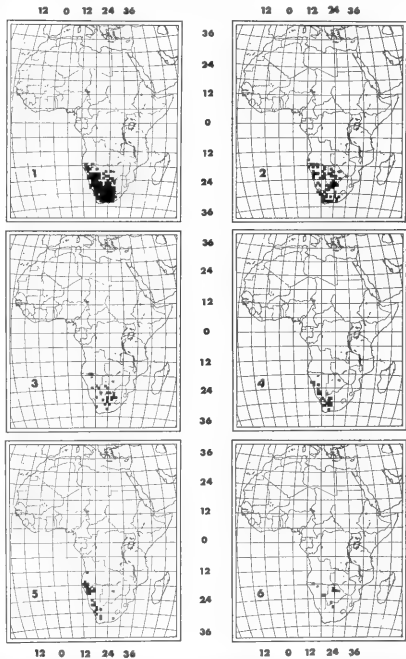


Fig. 2. Maps 1-6. Degree square diagrams showing the distribution of *Desmodillus auricularis* (sp. 33), *Gerbillus paebe* (sp. 34), *Malacothrix typica* (sp. 23), *Parotomys littledalei* (sp. 31), *Petromyscus collinus* (sp. 17) and *Zelotomys woosnami* (sp. 4).

range in a drier climate and a clear indicator of the present boundary between South West Arid and Savanna zones.

35. *Gerbillus vullinus* (No. Map; Table 2): Endemic in South West Arid. Restricted to Namib and Karoo (Bushmanland only).

36. *Tatera inclusa* (No Map; Table 3): Southern Savanna forest margins (?). Affinities with *T. brantsi*, status uncertain. Relict populations in S. Rhodesia (Mt. Selinda) and Mozambique (Gorongozo and elsewhere).

37. *Tatera afra* (Fig. 4, Map 13; Table 1): Endemic in South-West Cape. Distribution almost exactly determined by the Table Mountain Sandstone. Easterly extension along coast towards Port Elizabeth checked by soil change and George-Knysna forests. Distinct from *T. brantsi* but closer to it than *T. leucogaster* and bearing a distinct flea fauna (de Meillon *et al.* 1961). Geographically isolated from all other *Tatera*.

38. *Tatera brantsi* (Fig. 3, Map 11; Tables 2, 3): Sandy areas in Savanna and South West Arid, particularly the highveld grasslands and Kalahari. Isolated ssp. *miliaria* in sandy pockets in the Karoo; an isolated ssp. *namaquensis* on lower Orange River; ssp. *ruddi* isolated in Zululand coastal plain. Intrudes into the bushveld of the north-western Transvaal with the Waterberg Sandstone. Extends from the northern Kalahari up the Zambezi valley to Mongu. Prefers a lighter soil than *T. leucogaster* and does not extend from the fringes of the Kalahari westwards as *T. leucogaster* does.

39. *Tatera leucogaster* (Fig. 3, Map 13; Tables 2, 3): Southern Savanna woodlands and the Kalahari from the Orange River to the southern Congo and southern Tanganyika. Absent from dune country in the south-western Kalahari but penetrating the subdesert scrub and grass of the north-western fringes. An indicator of the boundary between Pole Evans' (1936) 'mixed grass' and 'short grass' in western Orange Free State and between bushveld and highveld grasslands of the Transvaal. Co-exists with *T. brantsi*, often using the same warrens but prefers to make burrows at the base of bushes and small trees rather than in the open like *T. brantsi*. Lives in sandy loam and lighter loam soils. Geographical variation in colour and size is fairly uniform and no isolated distinct subspecies can be defined.

(Note on the nomenclature employed: The generic and specific names are in conformity with the current revision of Southern African Muridae being done at the Medical Ecology Centre and the reasons for the changes are to be published elsewhere.)

CLASSIFICATION OF THE DISTRIBUTION PATTERNS OF MURIDAE

A general indication of some of the distribution patterns has already been given and the maps in Fig. 2-7 may be studied in conjunction with the notes on the species to gain an idea of the variety. In order to group the patterns an attempt has been made to compile a key—admittedly rather crude in its present form—which it is hoped in due course to expand to include the rest of the Rodentia and other small mammals. The subdivisions of the biotic zones will have, of course, to be defined more precisely in terms of vegetation types etc.

In so far as the Muridae are concerned it would appear that available habitats are the basic distribution factor to be taken into account, and that vegetation type, soil and topography—in that order—provide the means of definition better than the more 'distant' climatic factors.

DRAFT KEY* TO THE DISTRIBUTION PATTERNS OF MURIDAE OCCURRING IN SOUTHERN AFRICA (SOUTH OF KUNENE-ZAMBEZI AS DEFINED ON p. 57)

1	Confined to Southern Africa (with some minor crossings)	2
	Not confined to Southern Africa	20
2 (1)	Generally distributed throughout Southern Africa (Map 27)	<i>A. namaquensis</i>	(sp. 7)
	Not generally distributed in Southern Africa	3

DISTRIBUTION OF SOUTHERN AFRICAN MURIDAE; NOTES ON THEIR FOSSIL ANTECEDENTS

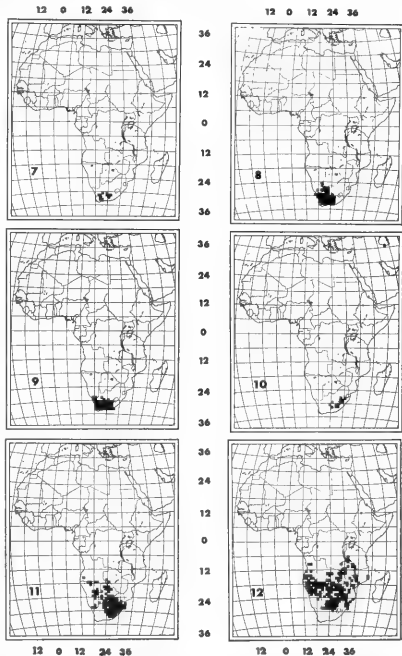


Fig. 3. Maps 7-12. Degree square diagrams showing the distribution of *Aethomys granti* (sp. 8), *Parotomys brantsi* (sp. 30), *Otomys unisulcatus* (sp. 28), *O. sloggetti* (sp. 39), *Tatera brantsi* (sp. 38) and *T. leucogaster* (sp. 39). *T. leucogaster* probably also occurs in eastern Angola and throughout Mozambique, as yet incompletely surveyed.

3 (2)	About equally distributed in South West Arid and Savanna, absent from Karoo proper and South-West Cape (Map 11)	<i>T. brantsi</i>	(sp. 38)
	Not so distributed		4
4 (3)	Primarily confined to South West Arid		5
	Not primarily confined to and may not occur in South West Arid; may occur in South-West Cape and/or Savanna		14
5 (4)	Generally distributed in South West Arid, with marginal extensions or relict ssp. in South-West Cape and Savanna		6
	Restricted distribution in South West Arid		8
6 (5)	Relict ssp. in South-West Cape and Savanna (Map 2)	<i>G. paebe</i>	(sp. 34)
	Marginal extensions into South-West Cape and Savanna		7
7 (6)	Common (Map 1)	<i>D. auricularis</i>	(sp. 33)
	Rare (Map 3)	<i>M. typica</i>	(sp. 23)
8 (5)	Restricted to Kalahari (Map 6)	<i>Z. woosnami</i>	(sp. 4)
	Not restricted to Kalahari		9
9 (8)	Restricted to western Escarpment and fringes		10
	Not so restricted, but not absent therefrom		12
10 (9)	Associated with mountainous areas (Map 5)	<i>P. collinus</i>	(sp. 17)
	Associated with sandy areas		11
11 (10)	Common, an isolated ssp. in northern Namib, apparently absent from southern Namib immediately south of Swakopmund (Map 4)	<i>P. littledalei</i>	(sp. 31)
	Very rare, locally common, found in northern and southern Namib (No Map)	<i>G. vallinus</i>	(sp. 35)
12 (9)	Mainly restricted to the Karoo, extending north of Orange River into southern Kalahari (Map 8)	<i>P. brantsi</i>	(sp. 30)
	Mainly restricted to Karoo but not extending to or just crossing Orange River	<i>A. granti</i>	(sp. 8)
13 (12)	Confined to Upper and Great Karoo (Map 7)		
	Throughout Karoo and fringes and just across Orange River to Luckhoff (Map 9)	<i>O. unisulcatus</i>	(sp. 28)
14 (4)	Common to parts (Upper Karoo) of South West Arid and parts of adjoining Savanna (Map 10)	<i>O. sloggetti</i>	(sp. 29)
	Absent from South West Arid, present in South-West Cape		15
15 (14)	Endemic in South-West Cape		16
	Relict in South-West Cape and occurring in Savanna grasslands		17
16 (15)	Distributed in sandy areas (Map 13)	<i>T. affra</i>	(sp. 37)
	Distributed in hilly areas		17
17 (16)	Confined to rocky sites (Map 15)	<i>A. subsplinosus</i>	(sp. 14B)
	Confined to grass-scrub (Map 14)	<i>P. verreauxi</i>	(sp. 6)
18 (15)	Occurring east of the Escarpment (Map 17)	<i>O. laminatus</i>	(sp. 24)
	Occurring on both sides of the Escarpment		19
19 (18)	Confined to the eastern Cape (Map 16)	<i>O. saundersiae</i>	(sp. 27)
	Occurring northwards from eastern Cape to Transvaal, Natal and Basutoland highveld and montane grasslands (Map 18)	<i>M. albicaudatus</i>	(sp. 32)
20 (1)	Southern and Northern Savanna and fringes to West Africa		21
	Southern Savanna towards or beyond equator, not to West Africa		27
21 (20)	Reaching South-West Cape down 'tropical corridor' or occurring there		22
	Not reaching the South-West Cape		25
22 (21)	Marginal invasion of extreme east end of South-West Cape from Savanna (Map 22)	<i>P. natalensis</i>	(sp. 5)
	Relict ssp. or populations in South-West Cape (peninsula area)		23
23 (22)	Not west of Natal Drakensberg, absent in South West Arid, funnels down south-east coast Savanna (Map 21)	<i>D. incomtus</i>	(sp. 11)
	Occurring in or marginal to South West Arid		24
24 (23)	Generally distributed in South West Arid (Map 26)	<i>M. minutoides</i>	(sp. 10)
	Marginal in South West Arid (Map 29)	<i>Steatomys</i> spp.	(sp. 18)
25 (21)	Reaching Uitenhage down 'tropical corridor', east of Natal Drakensberg (Map 23)	<i>T. dolichurus</i>	(sp. 1)
	Not further south than eastern Transvaal or southern Mozambique		26
26 (25)	Relict ssp. discontinuously distributed (in Southern Africa at least) ? in association with past or present forest areas (Map 35)	<i>C. gambianus</i>	(sp. 16)
	Relict ssp. in Transvaal lowveld, rare (No Map)	<i>D. nyikae</i>	(sp. 22)
27 (20)	Southern Savanna northwards through Sudan to North Africa (Map 15)	<i>Acomys</i> spp.	(sp. 14A)
	Southern Savanna northwards, not to N. Africa		28

DISTRIBUTION OF SOUTHERN AFRICAN MURIDAE; NOTES ON THEIR FOSSIL ANTECEDENTS

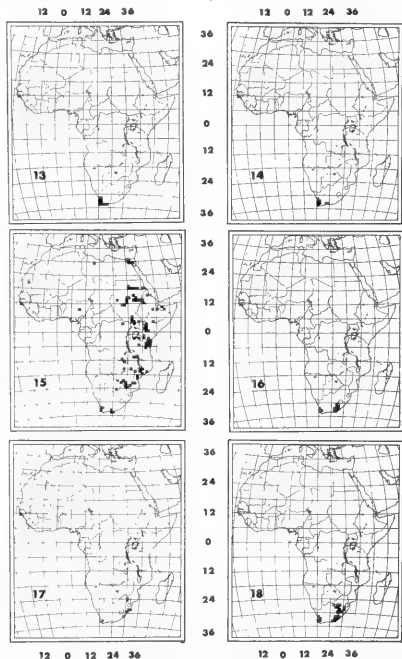


Fig. 4. Maps 13-28. Degree square diagrams showing the distribution of *Tatera afra* (sp. 37), *Praomys verreauxi* (sp. 6), *Acomys* spp. (sp. 14), *Otomys saundersiae* (sp. 27), *O. laminatus* (sp. 24) and *Mystromys albicaudatus* (sp. 32). The species of the genus *Acomys* await definition. The records in the South-West Cape are of the isolated species *A. subspinosus*.

28 (27)	Not reaching Sclater line; in South West Arid and Savanna from Orange River to southern Congo/Tanganyika (replaced in Tanganyika by <i>T. robusta</i> which goes north and west to Sudan and W. Africa) (Map 12)	<i>T. leucogaster</i>	(sp. 39)
	Reaching Sclater line		29
29 (28)	Not occurring south of the Limpopo Dry Belt (Map 36)	<i>P. fallax</i>	(sp. 12)
	Extending south of the Limpopo Dry Belt		30
30 (29)	In South West Arid and Savanna; marginal or relict in South-West Cape		31
	In Savanna, marginal in South West Arid, relict or absent in South-West Cape		32
31 (30)	Continues northwards from woodland and semi-desert, in woodland Savanna to north (northern Uganda) of the Sclater line (Map 25)	<i>S. camptstris</i>	(sp. 15)
	Continues northwards from grassland and semi-desert discontinuously in montane grasslands to Sclater line (Map 28)	<i>R. pumilio</i>	(sp. 9)
32 (30)	Funnelling down south-east coast to South-West Cape		33
	Funnelling down south-east coast but not to South-West Cape		34
33 (32)	Mainly attached to woodland habitats (Map 20)	<i>D. mesomelas</i>	(sp. 19)
	Mainly attached to grassland habitats (Map 19)	<i>D. melanotis</i>	(sp. 21)
34 (32)	Funnelling down to Transkei (Map 24)	<i>D. mystacalis</i>	(sp. 20)
	Funnelling down to southern Natal		35
35 (34)	Crossing westwards through Transvaal woodland but not far into South West Arid (Kalahari) (Map 33)	<i>O. angoniensis</i>	(sp. 26)
	Crossing westwards through Transvaal woodlands to Kalahari		36
36 (35)	Generally distributed in Kalahari northwards from Orange River (Map 34)	<i>T. paedulus</i>	(sp. 3)
	Restricted distribution from north-western Savanna into north-western Kalahari		37
37 (36)	Relict populations on eastern fringe of Kalahari (Kuruman, Vryburg) (Map 31)	<i>A. chrysophilus</i>	(sp. 2)
	Relict populations in central Kalahari (Map 32)	<i>L. griselda</i>	(sp. 13)

*The characteristics of the distribution pattern of any species can be noted by reading the key backwards from the key numbers in brackets in the lefthand column to the corresponding key numbers in the righthand column.

From the above key and distribution maps much can be gleaned, but it is beyond the scope of the present paper to probe much deeper into the way the present situation has been brought about. It is obvious that the present distribution of some of the Savanna species can be related to a wider Savanna area in the past during a pluvial period and, *vice versa*, that South West Arid species can be related to a wider desert area during a nonpluvial period. Equally important are the various stages of evolutionary advance revealed in the attainment of species, subspecies and 'isolated population' status by some forms; clearly an attempt can be made to account for these by considering the influence of climatic fluctuations and tectonic and other topographical changes on spread and survival. Some indications of the evolutionary history of the Muridae during the Pleistocene can be got by a comparison of the fossil murid fauna of the australopithecine deposits, incomplete though our knowledge is.

PRESENT DAY DISTRIBUTION PATTERNS AND PALAEOECOLOGY

It is now generally conceded that the Cricetinae have had a longer evolutionary history than the Murinae. Lavocat (1959) allies the Dendromurinae with the Cricetinae and traces their origin to the cricetodonts of the Miocene. He believes that the Murinae came later and originated in Asia, also from cricetodont stock.

Fossil murids from the Tertiary (Miocene and Pliocene) are scarcely represented in Southern Africa, but the record is better for the Pleistocene. While it is thus difficult at present to trace the origin of the subfamilies back to the Miocene it is possible to compare Pleistocene genera and species with those living at present.

Recent work on the microfauna found in the 'rodent breccia' associated with the australopithecine cave deposits in the north-west Cape (Taung) and the Transvaal (Sterkfontein area and Makapan) is beginning to produce a clearer picture of the species assemblages. The pioneer work of Broom has been furthered in recent years (Lavocat 1955, 1957; Davis

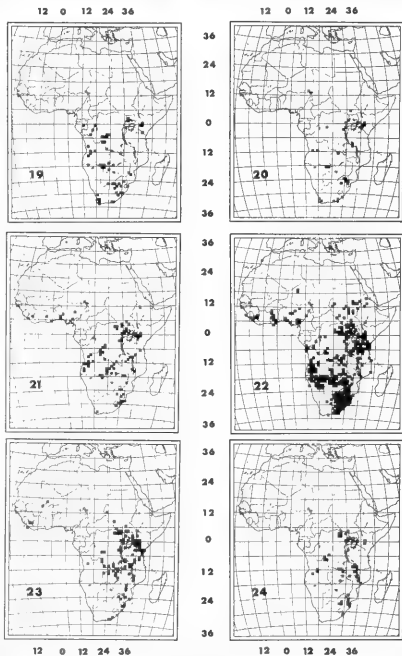


Fig. 5. Maps 19-24. Degree square diagrams showing the distribution of *Dendromus melanotis* (sp. 21), *D. mesomelas* (sp. 19), *Dasymys incomtus* (sp. 11), *Praomys natalensis* (sp. 5), *Thamnomys dolichurus* (sp. 1), and *Dendromus mystacalis* (sp. 20).

1959 and in press; de Graaff 1961) and we can now start to link up the lower Pleistocene murids (and other small mammals) with their living counterparts.

The early Pleistocene murids were, on the whole, not unlike those living in the same areas at the present day. Some species are clearly 'chronospecies', differing little from present day species; others are quite distinct and no modern counterparts are known, while others bear some resemblance to living species but differ in size and other details which suggest that a certain amount of subspeciation or even speciation combined with some extinction has intervened.

No subfamily of the Muridae living today is unrepresented in the early Pleistocene fauna, but the relative proportions of species and of individuals of a species, appear on present evidence to have been markedly different. Broom noted that the Cricetinae and Otomyinae were the dominant subfamilies in terms of numbers of individuals in the breccia. This is certainly the case in one reasonably complete sample of the microfauna that has been studied (see Davis 1959 for preliminary findings) which was collected by C. K. Brain from 18 ft. of decomposed breccia excavated at Kromdraai B in the Sterkfontein area.

THE KROMDRAAI B MURIDAE

This collection has now been worked through and is used here to make tentative comparisons between some of the fossil forms and their living counterparts. The discussion is admittedly speculative, since the identity of the fossil forms is difficult to establish on maxillary and mandibular fragments; it will take years of critical study and more complete specimens before it will be known whether even the few forms referred to here have been correctly interpreted.

The relative numbers, by subfamilies, of individuals and of number of species represented in the Kromdraai B collection are as follows:

Cricetinae	287 individuals of at least two species
Otomyinae	74 individuals of one species
Murinae	27 individuals of at least five species
Gerbillinae	10 individuals of two species
Dendromurinae	4 individuals of one species

The Cricetinae are now represented by *Mystromys albicaudatus*, which may be designated a chronospecies *M. hausleitneri*—*albicaudatus*. The other cricetine (a small species, larger than *M. darti*) is extinct (Davis in press). The *Otomys* (*O. gracilis*) no longer exists in the area, being replaced by two larger, near sibling species.

The Murinae are represented by a small and a larger *Mus*, the small one probably a chronospecies terminating in the living *M. minutoides*. The larger species has no living counterpart in Southern Africa except *Mus musculus*, which was introduced in comparatively recent times. Then there appear to be two species of *Dasymys*. *D. boliti* is apparently a chronospecies *boliti-incomtus*. The Dendromurinae are represented by a small *Dendromys*. The Gerbillinae have at least one species of *Tatera* and a *Desmodillus*.

PRESENT DISTRIBUTION OF EXTANT 'CHRONOSPECIES'

Subfamily Cricetinae

Mystromys hausleitneri—*albicaudatus* (Map 18, sp. 32): Widely but sparsely distributed in the Savanna grassland zone with an isolated population (? ssp.) in the South-West Cape. It still occurs in the Sterkfontein area.

Subfamily Otomyinae

Otomys (*Palaeotomys*) *gracilis* -? *O.* (*Myotomys*) *sloggetti turneri* (See Map 10, sp. 29). Confined to the north-eastern Orange Free State with related but distinct ssp. *robertsi* (Maluti

DISTRIBUTION OF SOUTHERN AFRICAN MURIDAE: NOTES ON THEIR FOSSIL ANTECEDENTS

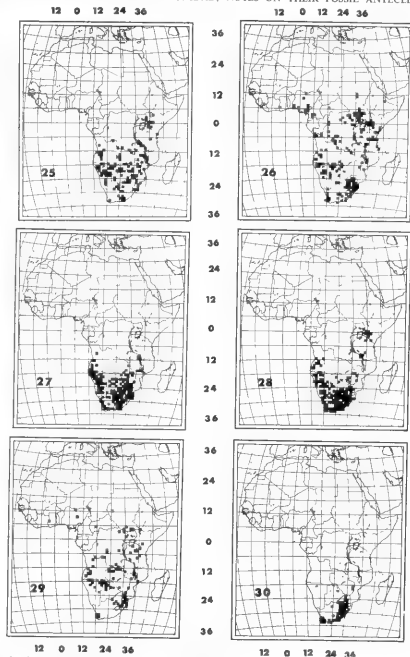


Fig. 6. Maps 25-30. Degree square diagrams showing the distribution of *Saccostomus campestris* (sp. 15), *Mus minutoides* (sp. 10), *Aethomys namaquensis* (sp. 7), *Rhabdomys pumilio* (sp. 9), *Steatomys* spp. (sp. 18) and *Otomys irroratus* (sp. 25). The species of the genus *Steatomys* await definition. The record in the South-West Cape are of the isolated form *S. pentonyx*. At least two species are represented in the Savanna zone.

Mountains), ssp. *jeppei* (eastern Cape) and spp. *sloggetti* (Karoo). It does not occur in the Sterkfontein area now, but is represented by two near sibling species *O. irroratus* and *O. angoniensis*. Although placed in different subgenera *O. gracilis* may prove to be nearer the living *O. angoniensis* than to *O. irroratus* since *O. sloggetti* and *O. angoniensis* (although differing in their molar lamina formula and other characters) have a similar arrangement of foramina for the entry of blood vessels and nerves into the bulla. There is clearly much to be done to unravel the post-early Pleistocene history of the Otomyinae, and climatic changes, with the attendant vegetation changes, will have to be invoked to account (a) for the present distribution of the genus and (b) of the speciation and subspeciation that has led to the present variety.

Subfamily Murinae

Mus cf. *minutoides*—*minutoides* (Map 26, sp. 10): Pan-African distribution and still occurs commonly in the Sterkfontein area.

Dasymys boliti—*incomtus* (Map 21, sp. 11): A swamp rat, typical of the Savanna, though its distribution in Southern Africa is local and discontinuous. *D. incomtus* does not now occur in the immediate vicinity of Sterkfontein, but has been found north of Pretoria and in the eastern Transvaal highveld.

Subfamily Gerbillinae

Tatera sp.—*brantsi* (Map 8, sp. 30): The Kromdraai B. fossil form is slightly smaller than present day *T. brantsi*. Two near sibling species now occur together in the Sterkfontein area: *T. brantsi* and *T. leucogaster* (= *schinzi*). Both have been trapped in the same warren a few hundred yards from Swartkrans. *T. leucogaster* overlaps with *T. brantsi* in the Kalahari and its fringes. When more fossil material is available it is suspected that two co-existing species will be found as is the case today (Davis in press).

Desmodillus cf. *auricularis*—*Desmodillus auricularis* (Map 1, sp. 33): This record is based on three mandibles, one with a first molar. Like the *Tatera*, the specimens are slightly smaller than present day *D. auricularis* and might possibly be a large *Gerbillus*. The nearest point of occurrence of *D. auricularis* to Sterkfontein is between Zeerust and Koster in the western Transvaal and near Hoopstad in the north-western Orange Free State. Evidently its occurrence at Kromdraai was marginal and possibly could be put down to relict populations surviving from a drier period with a Karoo vegetation. A possible limiting factor is its staple food plant—the so-called 'dubbeltjie' (seeds of *Tribulus terrestris*, Zygophyllaceae)—which flourishes around pans and along dry watercourses in the Karoo, Kalahari and their fringes.

Dendromus ? *antiquus*—? *melanotis* (Map 19, sp. 21): Of the four species of *Dendromus*—*mesomelas*, *mystacalis*, *melanotis* and *nyikae*—*D. mesomelas* is the largest and has not yet been found as a fossil. The other three are small and distinctions on tooth characters have not yet been worked out. Furthermore distribution data are somewhat scanty, so that it is not possible to comment at this stage on their relationship to the fossil forms. Since Lavocat now groups them and the Cricetinae in the family Cricetidae they are of special interest from the evolutionary and phylogenetic point of view.

It can thus easily be seen that with a picture in mind of the distribution patterns of even the living Muridae related to the species in this single deposit, it is possible to detect the influence of climatic changes on the species-composition and distribution of the ancestors of the living species. At the same time competition between ecologically equivalent species, such as between the cricetines and the murines, has clearly resulted in a change in the balance of the murid fauna. It is noteworthy that no small *Praomys* such as *P. verreauxi* or *P. natalensis* (*Myomys* and *Mastomys* auct.) has yet been certainly identified in the lower Pleistocene. Competition also seems to have been at work to restrict progressively the distribution of such forms as *Dasymys*, which are now sparsely and discontinuously distributed in Southern

DISTRIBUTION OF SOUTHERN AFRICAN MURIDAE; NOTES ON THEIR FOSSIL ANTECEDENTS

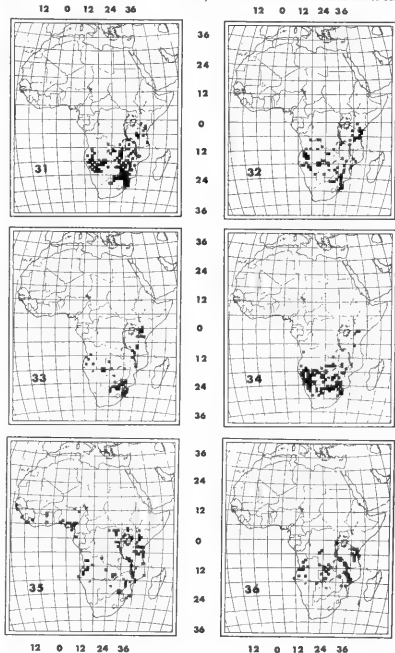


Fig. 7. Maps 31-36. Degree square diagrams showing the distribution of *Aethomys chrysophilus* (sp. 2), *Lemniscomys griselda* (sp. 13), *Otozomys angoniensis* (sp. 26), *Thallomys paedulus* (sp. 3), *Cricetomys gambianus* (sp. 16) and *Pelomys fallax* (sp. 12). *C. gambianus* is continuously distributed from east to west Africa (literature not fully searched for exact localities).

Africa and must have formerly been much more abundant and widespread. *Otomys* species and *Dasymys* co-existed and still co-exist, but *Otomys* is even more dominant over *Dasymys* forms now than the fossil evidence suggests for the lower Pleistocene. Possibly *Dasymys* was already losing its foothold at the time. This gets some support from the fact that a close relative of *Dasymys* is extinct, whereas most (but not all) species of *Otomys* are flourishing.

ACKNOWLEDGEMENTS

I wish to thank Mr. C. G. Coetzee for assistance in compiling the distribution data, Miss J. Walker for copying the maps and Mr. Max Ulrich for photographing them. This paper is published by permission of the Secretary for Health.

SUMMARY

The degree of attachment of the species of rodents of the family Muridae (occurring in Southern Africa) to the major biotic zones is analysed. It is shown that species-occurrence can be classified as endemic, near-endemic, marginal and relict. The main biotic zones, (based on vegetation types)—Savanna, South West Arid and South-West Cape—are further subdivided according to murid distribution patterns. A tentative attempt to link the fossil Muridae of the australopithecine cave deposits with living forms is made.

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DISCUSSION

Dr. Winterbottom: With reference to relict *Saccostomus* at Robertson, is it relevant that considerable areas in this district are karoid and many of the birds of Robertson are actually Karoo species and not South-West Cape forms.

Mr. Davis: It might be relevant, but we know so little about it, and this particular species is very plastic as regards its environment.

Dr. Bigalke: Murid distribution seems to be so neatly tied up with environment as to suggest that this group has been constant for a very long time and not much influenced by man.

J. MEESTER
TRANSSAAL MUSEUM,
PRETORIA.

The distribution
of *Crocidura* Wagler
in Southern Africa

The present paper summarizes the zoogeographic results obtained from a systematic revision of the genus *Crocidura* Wagler in southern Africa. The data on which these results are based form part of a more extensive report which is being published elsewhere (Meester, in press), and will not be repeated here in full. Keay's (1959) classification of vegetation types is followed. Rainfall distribution is taken from Wellington (1955).

Nine species are recognised: *Crocidura flavescens* (I. Geoffroy), *C. occidentalis* (Pucheran), *C. cyanea* (Duvernoy), *C. silacea* Thomas, *C. hirta* Peters, *C. luna* Dollman, *C. pilosa* Dobson, *C. bicolor* Bocage, and *C. maquassiensis* Roberts.

C. flavescens ranges from the south-western Cape Province, along the coast to the Eastern Province, inland to Lady Grey and perhaps Burgersdorp, further north along the coast to Durban district, and thence inland to the Maluti mountains in Basutoland and the Sabie district, eastern Transvaal (Fig. 1). A similar distribution pattern has been found in the case of various other species, such as *Myosorex varius* (Meester 1958: 326), *Amplorhinus multimaculatus*, the many-spotted snake, *Lycodonomorphus laevisissimus*, the African water snake, and *Philothamnus natalensis*, the Natal green water snake (Dr. V. F. FitzSimons, in litt.).

The range of *C. flavescens* falls entirely within the rainfall zone with an annual mean of 20 in. and over, with the exception of the dubious record from Burgersdorp. Most known localities further fall within the zone of 30 in. and over, and it appears that the colour of *C. flavescens* varies in response to variation in moisture conditions, being darker on the whole in the 30-plus in. zone than in the 20-30 in. zone.

No relationship is apparent with vegetation type. However, whatever vegetation type it inhabits, *C. flavescens* appears to frequent dense cover. For the rest it is normally found in broken country. On the eastern escarpment of the eastern Transvaal it ranges no further than the Sabie district, north of which, in the Olifants river valley, there is a break in the escarpment which may constitute a barrier to its spread. In the northern Transvaal and south-eastern Southern Rhodesia there is a more extensive break in the eastern escarpment, with lower rainfall (10-20 in. per annum) and different vegetation type from that found towards either the south or the north (woodland and savanna with abundant *Colophospermum mopane*—Keay 1959). This break doubtless prevents its ranging further north, and probably also acts as a barrier to the southward spread of *C. luna* and *C. occidentalis* (Fig. 2).

C. luna is confined in southern Africa to the eastern escarpment of Southern Rhodesia, where it extends as far south as the Melsetter district. *C. occidentalis* is sympatric with it in this area, and is further found at Mbambi on the Okavango. Both species are restricted to

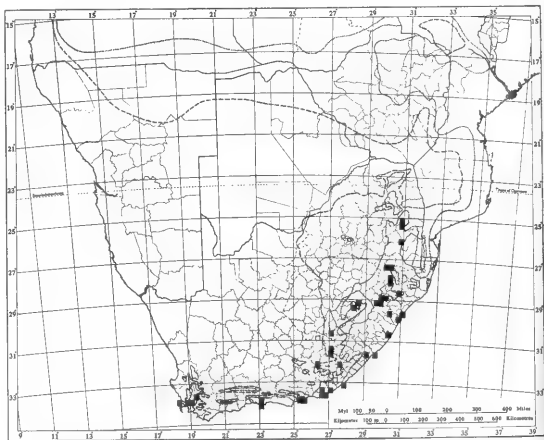


Fig. 1: Distribution of *Crocidura flavescens*. Solid squares represent authenticated records; dubious or literature records are represented by open squares. Broken line = 20 in. mean annual rainfall zone; dotted line = 30 in. mean annual rainfall zone.

a moist environment. Where they occur in Southern Rhodesia, mean annual rainfall is above 40 in. and, while the Okavango River runs through a drier area with a mean annual fall of 20–30 in., the habitat occupied by *C. occidentalis* (swamp vegetation) should meet the environmental requirements of a moisture-restricted species.

To these two species, perhaps even more than to *C. flavescens*, the dry conditions (and perhaps the different vegetation type) of the break in the eastern escarpment would constitute an effective barrier.

The failure of *C. occidentalis* to range further south in the western part of its southern African range can probably be explained on the same grounds. The Okavango runs through an only moderately moist area. Further south rainfall drops still further, to 10–20 in. per annum, and south of the Okavango swamp and Lake Ngami it would be impossible for this species to satisfy its environmental requirements by inhabiting the moist habitat offered by riverine or swamp vegetation. Probably, therefore, here as along the eastern escarpment it is prevented from ranging further south by the arid conditions it would encounter.

THE DISTRIBUTION OF *CROCIDURA* WAGLER IN SOUTHERN AFRICA

C. hirta extends from the extreme northern Cape Province in the west and Durban in the east, through Bechuanaland, north-eastern South West Africa, the Transvaal, Moçambique and Southern Rhodesia, to the Kunene and Zambezi rivers, and thence further north (Fig. 3). *C. bicolor* appears to have a roughly similar distribution, although locality records are few and scattered, and do not extend quite as far south as in the case of the other species. Neither species is represented in the extremely dry western part of South West Africa, with rainfall much below 8 in. (200 mm.) per annum.

In both *C. hirta* and *C. bicolor* colour variation in response to variation in moisture conditions has led to the establishment of moisture-adapted subspecies, a paler western dry-area form (*C. h. deserti* and *C. b. woosnami*), and a darker eastern moist-area form (*C. h. hirta* and *C. b. bicolor*). In both cases, furthermore, the subspecies boundary coincides roughly with the 20-in. or the 24-in. (600 mm.) mean annual rainfall zone (see also Meester 1959).

The eastern subspecies (particularly the widespread *C. h. hirta*) occupy diverse vegetation types, but mainly woodland and savanna; the western subspecies inhabit partly relatively dry,

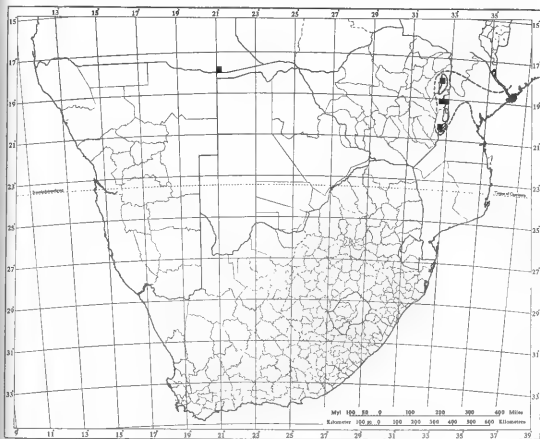


Fig. 2: Distribution of *Crocidura occidentalis* in southern Africa. Broken line = 40 in. mean annual rainfall zone; dotted line = 60 in. mean annual rainfall zone.

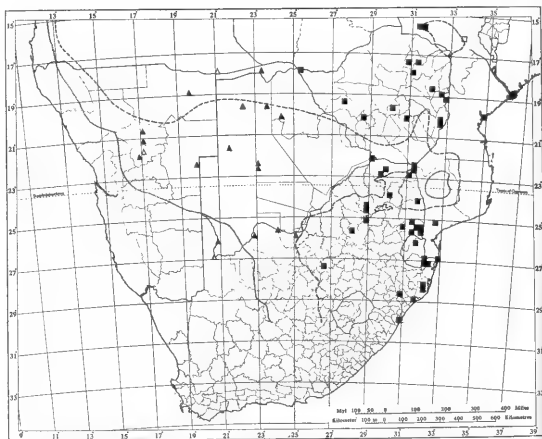


Fig. 3: Distribution of *Crocidura hirta* in southern Africa. Squares = *C. h. hirta*; triangles = *C. h. deserti*. Solid symbols represent authenticated records, while open symbols represent dubious or literature records. Dotted line = 10 in. mean annual rainfall zone; broken line = 20 in. mean annual rainfall zone.

undifferentiated woodland and savanna, and partly wooded steppe with abundant *Acacia* and *Commiphora* (Keay 1959).

C. cyanea has an extensive range in southern Africa, extending all the way from the Cape Peninsula to the Kunene and Zambezi rivers, with the exception only of the Namib Desert, with mean annual rainfall less than 5 in. It is unknown from some areas within this region, such as parts of the northern Cape Province, the Kalahari and Bechuanaland, but this may be the consequence merely of gaps in our knowledge of its distribution (Fig. 4).

In this species too, adaptation in response to variation in moisture conditions has led to the establishment of dry- and moist-area subspecies, and again the boundaries of the subspecies meet, where they do so, along the 20-in. mean annual rainfall zone. (In parts of their ranges the two subspecies are apparently geographically isolated, at least on present evidence). However, in this case the western arid-area form, *C. c. cyanea*, is only slightly paler than the eastern form, *C. c. infumata*, and differs mainly in being more grey and grizzled than the latter.

THE DISTRIBUTION OF CROCIDURA WAGLER IN SOUTHERN AFRICA

C. silacea ranges from Natal and Zululand to Swaziland, northward along the eastern escarpment to eastern and northern Transvaal, westward to the Pretoria district, the Transvaal highveld and Kanje, Bechuanaland, and further north to Southern Rhodesia and beyond. This range includes the three known records for *C. maquassiensis*, which may be the same animal. All available locality records for both species fall within the mean annual rainfall zone of 20 in. and over. Towards the south its range is limited in somewhat the same fashion as that of *C. h. hirta*.

C. pilosa occurs in southern Africa in two geographically completely isolated regions, in which two different subspecies are recognized (Fig. 5). *C. p. pilosa* ranges from Inhambane, Moçambique, to Mooi River, Natal in the south, and to Woodbush, northern Transvaal, Potchefstroom, Transvaal highveld, and Vredefort, Orange Free State in the west. An unconfirmed but probably authentic record further suggests that its range extends as far west as the junction of the Marico and Limpopo rivers.

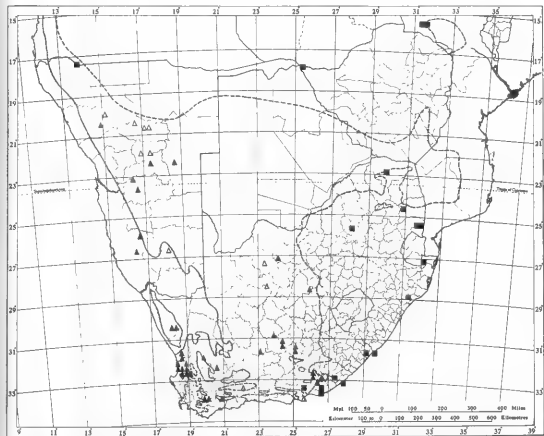


Fig. 4: Distribution of *Crocidura cyanea* in southern Africa. Triangles = *C. c. cyanea*; squares = *C. c. infumata*. Solid symbols represent authenticated records; dubious or literature records are represented by open symbols. Dotted line = 5 in. mean annual rainfall zone; broken line = 20 in. mean annual rainfall zone.

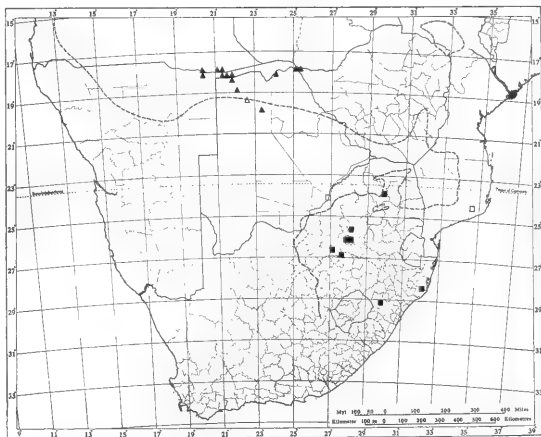


Fig. 5: Distribution of *Crocidura pilosa* in southern Africa. Squares = *C. p. pilosa*; triangles = *C. p. shortridgei*. Solid symbols represent authenticated records, while dubious or literature records are represented by open symbols. Broken line = 20 in. mean annual rainfall zone.

C. p. shortridgei is known in Southern Africa from the Okavango river in north-eastern South West Africa, the Caprivi strip and Ngamiland, and has also been collected in parts of Northern Rhodesia. This form is restricted roughly to the rainfall zone with an annual mean of 20 in. and over and so, apparently, is *C. p. pilosa*. Both subspecies occupy a moist environment. The geographic gap between their ranges, extending across the Kalahari desert and northern Bechuanaland, consists of a zone with lower rainfall (10–20 in. per annum), lacking the moist environmental conditions they appear to require. This suggests that their geographic isolation may be associated with an ecological barrier in moisture conditions extending across this area.

It is not clear why *C. pilosa* does not occur in Southern Rhodesia, where favourable environmental conditions for its survival would appear to prevail. It is further not clear why this species, and also *C. hirta*, *C. bicolor* and *C. silacea*, range no further south than they do. They do not appear to be limited by either rainfall, vegetation or topographic barriers; indeed the eastern coastal belt forms a corridor for the southward spread of a number of

species, like *C. flavescens*, *Myosorex varius*, *M. cafer* (see Meester, 1958) and others. *C. pilosa* and *C. silacea* have a somewhat restricted range, and *C. bicolor*, although widespread, is not a very common species. *C. hirta*, however, not only occurs throughout a wide range of environmental conditions, but is the most common species of *Crocidura* in those areas in southern Africa where it is found. Why this species, at least, spreads no further south remains a mystery.

From the above it appears that *Crocidura* is very widespread in southern Africa, and that it occupies a variety of habitats, ranging from the extremely moist eastern escarpment of Southern Rhodesia, in parts of which mean annual rainfall exceeds 60 in., to the dry west, in areas with mean annual rainfall between 5 and 10 in. The only part of southern Africa whence it has not been recorded is the Namib Desert of South West Africa, with mean annual rainfall less than 5 in.

A widespread distribution of this nature might suggest a group that is little affected by environmental conditions. However, in fact it appears that environmental factors, notably moisture, play a prominent part in determining the distribution and nature of the species dealt with. Particularly a zone corresponding roughly with the 20-in. mean annual rainfall zone (or the 24-in. (600 mm.) zone, which follows more or less the same course), appears to be of great importance. Of the forms considered only *C. c. cyanea*, *C. h. deserti* and *C. b. woosnami* occur extensively in the below 20-in. zone, while *C. flavescens*, *C. silacea*, *C. pilosa* and the subspecies *C. c. infumata*, *C. h. hirta* and *C. b. bicolor* are virtually or entirely restricted to the zones above 20- or 24-in. In *C. cyanea*, *C. hirta* and *C. bicolor*, furthermore, in each of which one of the two recognized subspecies is a dry-area form (*C. c. cyanea*, *C. h. deserti* and *C. b. woosnami*), while the other occurs in moister areas (*C. c. infumata*, *C. h. hirta* and *C. b. bicolor*), the boundaries between subspecies coincide roughly with the 20- or 24-in. zone. In *C. pilosa* the two subspecies *C. p. pilosa* and *C. p. shorridgei* are both confined roughly to the 20-in. zone, and the intervening area with lower rainfall (10-20 in. per annum) appears to act as an ecological barrier.

C. luna and *C. occidentalis* appear to be restricted to an even moister environment, with mean annual rainfall above 40 in. (except where *C. occidentalis* occurs along the Okavango, in a very moist habitat). This may to some extent be true also of *C. flavescens* as this species, although occurring in the 20-30 in. zone, is for the most part found in the 30-in. zone.

In view of the important rôle of moisture in determining range limits, it is not surprising to find that it is also responsible for some variation in colour in several species. In *C. flavescens* colour is darker in the 30-in. zone than in the 20-30-in. zone. The same is the case in *C. h. hirta*. In *C. hirta* and *C. bicolor*, furthermore, the dry-area subspecies (*C. h. deserti* and *C. b. woosnami*) is in each case strikingly paler than the moist-area form (*C. h. hirta* and *C. b. bicolor*).

Thus, all three species illustrate Gloger's rule, that colour is darker in warm, moist areas than in cold or arid regions. In *C. cyanea*, however, although the dry-area form (*C. c. cyanea*) is slightly paler than that from the moister region (*C. c. infumata*) the main difference between the two forms is that *C. c. cyanea* is greyer and more grizzled than *C. c. infumata*. Doubtless this also represents an adaptation to variation in moisture conditions, following however an unusual pattern.

To some extent the forms here considered are associated with particular vegetation types, but this is probably a consequence merely of the fact that these vegetation types are similarly restricted to particular rainfall zones. Broadly speaking the western steppe country of southern Africa falls within the 5-20-in. mean annual rainfall zone, while in the 20-plus-in. zone the vegetation type is mainly temperate and subtropical grassland or woodland and savanna, with specialized types occurring in certain areas, such as high mountains and the coastal regions (Keay 1959). The forms occurring in the 5-20-in. zone, therefore, are found mainly

in steppe country, while those occurring in the 20-in. zone inhabit woodland and savanna, temperate and subtropical grassland, montane forests, the coastal forest-savanna mosaic, and the like.

C. flavescens, *C. luna* and *C. occidentalis* (in part) appear to be confined to mountainous regions, such as the eastern escarpment. However, this may be merely a consequence of moisture-restriction and perhaps a preference for dense cover. Both requirements would be met by the moist conditions and lush vegetation of the eastern escarpment, and particularly of the densely-vegetated mountain streams found along it.

It thus appears that the wide distribution of *Crociodura* in southern Africa is a consequence not of its being little affected by environmental factors, but of its success in adapting to these factors. Of the known forms only *C. flavescens* and possibly *C. maguassiensis* (if it is a valid species) may have originated locally. The other species almost certainly colonized southern Africa from East and Central Africa. As such they were probably all adapted to an at least moderately moist environment (with mean annual rainfall above about 20 in.), as indeed is the case with most of the forms at present known from southern Africa. The forms occurring in dry areas (*C. h. deserti*, *C. b. woosnami* and *C. c. cyanea*) therefore probably represent secondary adaptations to arid conditions, arising from stocks which were primarily adapted to a moister environment.

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DISCUSSION

- Dr. Poynton*: It seems possible that the limits of distribution in some of the northern *Crociodurids* may be related to temperature and it might therefore be useful to consult an isotherm map.
Dr. Meester: I have done so, but so far no close correlation emerges.
Dr. Stuckenberg: What fossil record is there or other evidence of similar species occurring in the Pleistocene?
Dr. Meester: There are some similar species to be found at Taung and some at Sterkfontein. *Crociodura hirta* occurs at Taung in the Middle Stone Age strata.
Prof. Ever: Is there any clear specificity in feeding habits which might explain distribution?
Dr. Meester: This is difficult to determine. Stomach contents are generally too well digested to yield many identifiable chitinous fragments and in some limited work on captive animals it has proved easier to discover what they do not eat than what they do.

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On the status and
distribution of
ungulate mammals
in the Cape Province,
South Africa

INTRODUCTION

The present status and distribution of ungulate mammals—and indeed of practically all other members of the class—in South Africa is imperfectly known. The broad zoogeographical outlines have long been established (Sclater and Sclater, 1899), but precise detailed information is still lacking, particularly for the huge land area, most of it farmed, lying outside the National Parks and Game Reserves.

In the most recent works of reference, Roberts (1951) and Ellerman *et al.* (1953), as much detail as was available to the authors is included. But for the Republic of South Africa there is no work comparable in scope with that of Shortridge (1934) on South West Africa except Sclater (1900), which is still useful but in many ways out-of-date. Kettlitz (1955) has published a valuable account of some Transvaal game animals and recent papers dealing with South West Africa (Bigalke, 1958), Southern Rhodesia (Fraser, 1958) and Northern Rhodesia (Grimwood *et al.*, 1958 and Ansell, 1960) are available. That of Knobel (1958) on the Union (now Republic) of South Africa gives little information on land outside Parks and Reserves and is in some respects misleading.

Narrowing the field down to the Cape Province, there is only the early work of Hewitt (1931) and the short but interesting paper by Rand (1955). The work reported in the present preliminary paper represents an attempt to remedy the deficiency for a part of this Province. Further papers are planned, some of which will also deal with groups other than ungulates.

METHODS

The idea of a questionnaire survey was that of C. J. Skead, who put it into operation whilst Director of the Kaffrarian Museum. Essentially it was devised as a method of collecting facts about the status of "game" and "vermin" upon which rational conservation and control measures could be based. On his arrival at King William's Town one of us (J.A.B.) took over this work with a view to covering all farms in the eastern Cape region. The other took up the study for the northern Cape from the McGregor Museum. The aim of surveying the entire Province has not yet been realised, but 55 of the 96 administrative units under the control of Divisional Councils have now been dealt with and the results form the basis of this paper.

The survey investigated a number of larger mammals of which only the ungulates will be considered here. For practical convenience two groups were created, viz.

(A) Those large, obvious and well-known "game" antelope the numbers of which a farmer could reasonably be asked to estimate and which we expected to be present in our respective areas. From a conservationist's point of view the status of these forms is of particular interest.

(B) Other species, equally well-known to the farmer, the habits or habitats of which make the estimation of population almost impossible.

For (A) the farmer was asked to estimate the number of each species on his property, while for (B) he was merely requested to state whether or not each was present. Table 1 shows the species which comprised these groups.

TABLE 1.

UNGULATES LISTED ON THE QUESTIONNAIRES

GROUP A (Numbers asked for).

Oribi	<i>Ourebia ourebi</i>	(King)
Klipspringer	<i>Oreotragus oreotragus</i>	(Both)
Vaal Ribbok	<i>Pelea capreolus</i>	(Both)
Rooi Ribbok	<i>Redunca fulvorufula</i>	(Both)
Springbok	<i>Antidorcas marsupialis</i>	(Both)
Blesbok	<i>Damaliscus dorcas phillipsi</i>	(Both)
Hartebeest	<i>Alcelaphus buselaphus</i>	(McG)
Black Wildebeest	<i>Connochaetes gnou</i>	(McG)

GROUP B (Presence or absence asked for).

Aardvark	<i>Orycteropus afer</i>	(Both)
Dassie	<i>Procavia capensis</i>	(Both)
Tree Dassie	<i>Dendrohyrax arboreus</i>	(King)
Bush Pig	<i>Potamochoerus porcus</i>	(King)
Blue Duiker	<i>Cephalopus monticola</i>	(King)
Duiker	<i>Sylvicapra grimmia</i>	(Both)
Steenbok	<i>Raphicerus campestris</i>	(Both)
Grysbok	<i>Raphicerus melanotis</i>	(King)
Bushbuck	<i>Tragelaphus scriptus</i>	(King)
Kudu	<i>Tragelaphus (Strepsiceros) strepsiceros</i>	(Both)

The nomenclature is that of Ellerman *et al* (1953).

Key to third column:

King: Kaffrarian Museum questionnaires only.

McG: McGregor Museum questionnaires only.

Both: on both questionnaires.

From the table it will be seen that a number of Cape ungulates were not listed. These were species known to be extinct or thought to be restricted to National Parks and Reserves. In most of the Kaffrarian Museum questionnaires and in all those sent from the McGregor Museum, farmers were asked to mention antelopes not listed on the forms. This resulted in some quite unexpected species being recorded, most of them introduced by interested farmers. An additional section of the questionnaire sought information on lambing (kidding) seasons in antelope. This will not be discussed here.

Results were calculated as follows. For all animals in each Division the ratio of the number of returns recording the species as present to the total number of completed questionnaires received was expressed as a percentage. Thus in the Aberdeen Division, of 36 completed questionnaires received, 25 reported the presence of Duiker. Evaluated as a percentage, this gives the figure 69.5 (Table 3). We have called this the "percentage occurrence". In addition, for animals in group (A), the farmers' numerical estimates were summed for each Division.

RESULTS

The data obtained from the questionnaires is summarised in Tables 2 and 3.

STATUS AND DISTRIBUTION OF CAPE UNGULATES, SOUTH AFRICA

TABLE 2.
PERCENTAGE OCCURRENCE (*) OF CERTAIN UNGULATES IN 55 DIVISIONS OF THE
PROVINCE OF THE CAPE OF GOOD HOPE, SOUTH AFRICA

Division	Aardvark	Dassie	Tree Dassie	Mt. Zebra	Bush Pig	Warthog
Aberdeen	94.5	83.4	13.9	—	—	—
Adelaide	—	84.5	39.6	1.7	31.1	—
Albany	67.5	82.0	24.8	—	50.4	—
Alexandria	59.5	40.5	57.2	—	64.3	—
Aliwal North	82.4	98.6	6.8	—	—	—
Barkly East	—	98.0	—	—	—	—
Barkly West	51.9	10.1	—	—	—	—
Bathurst	55.0	65.0	70.5	—	42.9	—
Bedford	—	82.4	33.4	—	31.4	—
Britstown	96.2	92.3	—	—	—	—
Burgersdorp	82.9	75.6	2.4	—	—	—
Cathcart	80.4	91.5	5.6	—	8.5	—
Colesburg	94.5	96.4	9.1	—	—	—
Cradock	91.3	83.7	4.4	1.9	1.9	—
De Aar	97.1	94.1	—	—	—	—
Dordrecht	50.0	90.0	4.0	—	—	—
East London	87.1	51.5	29.0	—	3.1	—
Elliott	5.6	97.1	12.5	—	—	—
Fort Beaufort	—	83.3	23.4	—	50.0	—
Gordonia	77.6	40.8	—	—	—	—
Graaff Reinet	96.3	94.4	6.6	—	4.7	—
Hanover	91.9	95.9	—	—	—	—
Hay	64.1	61.5	—	—	—	—
Herbert	67.3	52.2	—	—	—	—
Herschel	25.0	100.0	—	—	—	—
Hofmeyr	83.4	80.5	5.5	—	—	—
Hopetown	95.6	71.1	—	—	—	—
Humansdorp	57.8	77.8	6.7	—	25.5	—
Jansenville	89.1	86.5	16.2	—	10.8	—
Kimberley	62.1	37.1	—	—	—	—
King William's Town	85.8	71.5	53.6	—	†	—
Komga	96.1	73.0	73.0	—	9.6	—
Kuruman	91.7	15.7	—	—	—	—
Lady Grey	60.0	100.0	3.3	—	—	—
Maclear	27.1	95.9	6.2	—	—	—
Middelburg	95.5	93.3	5.6	—	—	—
Molteno	89.4	95.9	—	—	—	—
Pearston	100.0	90.0	10.0	—	25.0	—
Peddie	66.6	60.6	9.1	—	18.2	—
Philipstown	97.6	95.1	—	—	—	—
Port Elizabeth	33.3	33.3	22.2	—	100.0	—
Postmasburg	77.1	48.6	—	—	—	—
Queenstown	78.3	90.4	1.2	—	1.2	—
Somerset East	68.4	88.4	8.4	—	25.2	—
Sterkstroom	87.5	92.5	—	—	—	—
Steynsberg	85.5	83.5	—	—	—	—
Steytlerville	91.6	87.5	12.5	—	20.8	—
Stutterheim	80.0	75.5	24.4	—	17.8	—
Tarkastad	86.4	88.1	3.4	—	—	—
Uitenhage	74.4	58.9	33.3	—	84.5	—
Uniondale	45.1	93.5	6.4	—	12.9	—
Venterstad	77.8	83.4	—	—	—	—
Victoria East	74.0	52.2	17.8	—	47.8	—
Vryburg	71.0	0.6	—	—	1.2	0.6
Willowmore	81.1	70.7	3.4	—	—	—

* see text for explanation

† King William's Town division has Bush Pig although the survey produced no records

TABLE 2 (contd.i)

Division	Blue Duiker	Duiker	Steen- bok	Grys- bok	Oribi	Klip- springer	Vaal Ribbonk	Rooi Ribbonk
AB	—	69.5	97.3	2.8	—	11.1	11.1	19.4
AD	25.8	93.1	58.6	5.2	—	1.7	25.8	39.6
ALB	34.9	93.0	51.9	49.6	3.1	—	3.1	10.1
AL	45.0	81.0	21.0	73.8	11.9	—	2.7	4.8
A.N.	1.4	1.4	27.0	4.1	1.4	—	45.9	33.8
B.E.	—	—	4.1	38.8	—	—	69.4	75.5
B.W.	—	96.2	91.1	—	—	—	1.3	—
BAT	57.0	100.0	25.0	35.0	35.0	—	—	—
BED	17.6	90.2	82.4	15.7	—	—	45.1	72.5
BRI	—	11.5	100.0	—	—	7.7	—	—
BUR	—	—	46.4	—	—	—	29.2	46.3
CAT	2.8	23.9	9.8	2.8	—	—	28.2	21.1
COL	—	16.3	83.6	—	—	1.8	38.2	51.0
CRAD	1.9	54.4	81.5	1.9	—	13.1	33.7	41.3
D.A.	—	8.8	88.2	—	—	14.7	26.5	5.9
DORD	—	—	2.0	16.0	—	—	50.0	26.0
E.L.	67.7	80.6	12.9	12.9	—	—	—	3.1
ELL	—	2.8	5.6	11.2	—	—	5.6	5.6
F.B.	6.7	76.6	26.6	12.0	—	—	20.0	10.0
GOR	—	61.2	93.9	—	—	20.4	—	—
G.R.	0.9	57.0	86.0	3.7	—	39.2	36.4	42.1
HAN	—	—	89.9	—	—	2.0	14.3	4.1
HAY	—	74.4	97.4	—	—	5.1	—	—
HBT	—	52.2	95.6	—	—	1.8	7.9	2.7
HER	—	50.0	25.0	75.0	—	25.0	25.0	—
HOF	—	19.4	88.9	—	—	16.8	13.9	30.6
HOP	—	40.0	100.0	—	—	2.2	13.3	4.4
HUM	55.5	79.0	32.1	86.6	5.5	21.1	32.2	22.1
JAN	2.7	78.4	83.8	27.1	2.7	5.4	—	—
KIM	—	90.3	95.2	—	—	—	11.3	4.8
KWT	75.0	82.1	10.7	17.8	—	—	—	3.6
KOM	88.5	94.2	13.5	34.6	—	—	7.7	7.7
KUR	—	99.1	100.0	—	—	2.8	5.6	0.9
L.G.	—	—	3.3	13.6	3.3	—	36.7	50.0
MAC	—	—	—	2.8	2.8	—	10.4	8.3
MID	—	31.4	85.4	—	—	19.1	50.5	37.1
MOL	—	2.1	21.6	—	—	2.1	53.2	36.2
PEA	—	85.0	100.0	20.0	—	30.0	5.0	5.0
PED	48.5	94.0	51.5	27.3	—	3.2	3.3	3.3
PHIL	—	4.9	90.2	—	—	—	12.2	—
P.E.	66.7	89.0	33.3	77.9	—	—	—	—
POS	—	93.3	95.2	—	—	18.1	7.6	1.9
Q	1.2	32.5	37.4	—	—	1.2	32.5	54.2
S.E.	7.6	87.4	98.5	27.4	—	14.7	18.9	23.1
STE	—	5.0	20.0	—	—	—	47.5	50.0
STEY	—	5.8	69.9	—	—	7.8	38.8	64.1
ST	4.2	79.2	87.5	58.4	—	62.5	12.5	20.8
STUT	20.0	75.5	8.9	—	—	—	—	22.2
TARK	—	8.5	61.0	—	—	10.2	44.1	76.2
UIT	25.6	100.0	28.2	82.0	—	15.4	7.7	17.9
UN	6.4	90.4	51.6	93.5	—	77.5	83.9	6.4
VEN	—	5.5	77.8	—	—	—	44.4	61.1
V.E.	17.4	82.5	60.9	26.1	—	—	—	—
VRY	—	93.8	96.3	—	—	—	—	—
WILL	1.7	60.3	82.7	10.3	—	31.1	15.5	17.2

STATUS AND DISTRIBUTION OF CAPE UNGULATES, SOUTH AFRICA

TABLE 2 (contd. ii)

Division	Spring-bok	Gems-bok	Bles-bok	Harte-beest	Bl. Wilde-beest	Bush-buck	Kudu	Eland
AB	86.1	—	19.4	—	—	—	63.9	—
AD	36.4	—	20.7	—	—	63.8	34.4	—
ALB	8.5	—	4.7	—	—	70.5	39.8	—
AL	4.8	—	—	—	—	78.5	—	—
A.N.	6.8	—	9.5	—	—	—	—	—
B.E.	—	—	6.1	—	—	—	—	—
B.W.	11.4	—	3.8	2.5	—	—	31.6	1.3
BAT	—	—	—	—	—	83.2	—	—
BED	74.5	—	25.4	—	1.9	52.9	21.3	—
BRI	69.2	—	7.7	—	—	—	—	—
BUR	58.6	—	41.5	—	—	—	—	—
CAT	9.8	—	25.1	—	—	4.2	—	—
COL	72.8	—	18.2	—	—	—	—	—
CRAD	58.7	—	19.6	—	—	—	—	—
D.A.	82.4	—	14.7	—	—	—	—	—
DORD	6.0	—	14.0	—	—	—	—	—
E.L.	—	—	—	—	—	80.1	—	—
ELL	—	—	—	—	—	2.8	—	—
F.B.	6.7	—	6.7	—	—	63.3	23.1	—
GOR	51.0	16.3	6.1	2.0	2.0	—	6.1	6.1
G.R.	67.3	—	16.8	—	—	0.9	43.9	—
HAN	85.6	—	20.4	—	—	—	—	—
HAY	56.4	3.8	20.5	—	—	—	16.7	2.6
HBT	66.4	1.8	23.9	1.8	1.8	—	20.4	0.9
HER	—	—	—	—	—	—	—	—
HOF	80.5	—	5.5	—	—	—	—	—
HOP	75.6	—	13.3	—	—	—	2.2	—
HUM	—	—	—	—	—	68.9	—	—
JAN	45.9	—	—	—	—	2.7	64.9	—
KIM	80.0	1.6	16.1	9.7	3.2	—	17.7	3.2
KWT	—	—	—	—	—	75.0	—	—
KOM	—	—	—	—	—	98.0	—	—
KUR	36.1	5.7	1.9	8.3	—	—	0.9	2.8
L.G.	3.3	—	3.3	—	—	—	—	—
MAC	—	—	—	—	—	—	—	—
MID	75.3	—	15.7	—	—	—	—	—
MOL	8.5	—	8.5	—	—	—	—	—
PEA	65.0	—	—	—	—	—	75.0	—
PED	—	—	3.3	—	—	75.8	21.2	—
PHIL	85.4	—	26.8	—	2.4	—	—	2.4
P.E.	11.1	—	11.1	—	—	66.7	—	—
POS	50.5	0.9	14.3	—	—	—	0.9	2.9
Q	15.7	—	19.3	—	—	—	—	—
S.E.	69.5	—	16.8	—	—	23.2	55.8	—
STE	10.0	—	25.0	—	—	—	—	—
STEY	81.5	—	31.1	—	—	—	—	—
ST	58.4	—	12.5	—	—	4.2	95.8	—
STUT	—	—	2.2	—	—	46.7	2.2	—
TARK	54.2	—	33.9	—	—	—	—	—
UIT	—	—	—	—	—	69.2	38.5	—
UN	—	—	—	—	—	—	3.2	—
VEN	66.8	—	38.9	—	—	—	—	—
V.E.	4.4	—	8.7	—	—	69.6	52.2	—
VRY	13.0	—	5.6	8.6	—	—	1.2	0.6
WILL	48.3	—	13.8	—	—	—	39.6	—

Note: Abbreviations of Divisions as in Table 3.

TABLE 3.
POPULATION ESTIMATES OF CERTAIN UNGULATES REPORTED FROM 55 DIVISIONS
OF THE PROVINCE OF THE CAPE OF GOOD HOPE, SOUTH AFRICA

Division	Abbreviation	Oribi	Klip-springer	Vaal Ribbok	Rooi Ribbok
Aberdeen	AB	—	100	105	181
Adelaide	AD	—	—	220	1114
Albany	ALB	8	—	32	326
Alexandria	AL	13	—	12	14
Aliwal North	A.N.	—	—	424	229
Barkly East	B.E.	—	—	431	977
Barkley West	B.W.	—	—	—	—
Bathurst	BAT	63	—	—	—
Bedford	BED	—	—	962	1723
Britstown	BRI	—	25	—	—
Burgersdorp	BUR	—	—	56	601
Cathcart	CAT	—	—	279	310
Colesburg	COL	—	6	401	874
Cradock	CRAD	—	151	428	1181
De Aar	D.A.	—	65	108	120
Dordrecht	DORD	—	—	195	199
East London	E.L.	—	—	—	4
Elliott	ELL	—	—	6	6
Fort Beaufort	F.B.	—	—	61	80
Gordonia	GOR	—	112	—	—
Graaff Reinet	G.R.	—	516	852	3671
Hanover	HAN	—	15	77	22
Hay	HAY	—	98	—	—
Herbert	HBT	—	10	164	11
Herschel	HER	—	5	6	—
Hofmeyr	HOF	—	61	36	456
Hopetown	HOP	—	8	76	19
Humansdorp	HUM	29	258	352	210
Jansenville	JAN	—	30	—	—
Kimberley	KIM	—	—	99	78
King William's Town	KWT	—	—	—	—
Komga	KOM	—	—	39	35
Kuruman	KUR	—	11	75	5
Lady Grey	L.G.	6	—	326	256
Maclear	MAC	2	—	45	48
Middelburg	MID	—	237	932	988
Molteno	MOL	—	5	357	219
Pearston	PEA	—	102	5	30
Peddie	PED	—	6	—	—
Philipstown	PHIL	—	—	54	—
Port Elizabeth	P.E.	—	—	—	—
Postmasburg	POS	—	236	94	14
Queenstown	Q	—	—	234	956
Somerset East	S.E.	—	187	218	1035
Sterkstroom	STE	—	—	414	277
Steynsberg	STEY	—	18	362	851
Steytlerville	ST	—	420	14	54
Stutterheim	STUT	—	—	—	161
Tarkastad	TARK	—	34	754	1391
Uitenhage	UIT	—	41	11	229
Uniondale	UN	—	578	411	13
Venterstad	VEN	—	—	134	207
Victoria East	V.E.	—	—	—	—
Vryburg	VRY	—	—	—	—
Willowmore	WILL	—	475	89	93
Total		121	3810	9950	19268

STATUS AND DISTRIBUTION OF CAPE UNGULATES, SOUTH AFRICA

TABLE 3 (contd.)

Division	Springbok	Blesbok	Hartebeest	Black Wildebeest
AB	2,139	75	—	—
AD	449	281	—	—
ALB	1,045	215	—	—
AL	15	—	—	—
A.N.	28	150	—	—
B.E.	—	114	—	—
B.W.	1,216	36	5	—
BAT	—	—	—	—
BED	3,661	479	—	—
BRI	2,426	72	—	—
BUR	927	230	—	—
CAT	300	551	—	—
COL	3,946	351	—	—
CRAD	4,044	376	—	—
D.A.	6,726	101	—	—
DORD	22	127	—	—
E.L.	—	—	—	—
ELL	—	—	—	—
F.B.	100	115	—	—
GOR	4,136	25	6	1
G.R.	6,125	353	—	—
HAN	4,675	268	—	—
HAY	1,604	130	—	—
HBT	6,863	359	5	8
HER	—	—	—	—
HOF	1,768	17	—	—
HOP	3,701	63	—	—
HUM	—	—	—	—
JAN	617	—	—	—
KIM	11,407	512	312	16
KWT	—	—	—	—
KOM	—	—	—	—
KUR	3,116	17	108	—
L.G.	3	9	—	—
MAC	—	—	—	—
MID	5,556	928	—	—
MOL	192	132	—	—
PEA	1,496	—	—	—
PED	—	10	—	—
PHIL	3,564	339	—	9
P.E.	2	2	—	—
POS	3,137	152	—	—
O	175	348	—	—
S.E.	3,359	475	—	—
STE	65	113	—	—
STAY	2,774	550	—	—
ST	479	21	—	—
STUT	—	3	—	—
TARK	1,000	387	—	—
UIT	—	—	—	—
UN	—	—	—	—
VEN	374	193	—	—
V.E.	—	14	—	—
VRY	1,615	135	624	—
WILL	986	62	—	—
Total	95,833	8,890	1,060	34

Note: The Abbreviations used in the second column of p. 1 of this table are the same as those in Table 2 and on the maps.

DISCUSSION

(a) Evaluation of Method

A point not yet raised is the coverage obtained by the questionnaires. In all, 11,824 forms were sent out and 3057 were completed and returned, a percentage return of 25.9. In general, it is probably a fair assumption that farmers sufficiently interested in wild life to maintain or re-introduce it on their properties will have filled in their questionnaires. Conversely, those with little or no wild life will not have returned the forms. The conclusion to be drawn from this argument is that, although only one-quarter of the farmed land of the Divisions concerned is represented by our results, the animal population of this fraction is, in fact, more nearly the population of all the land. It is practically impossible to decide whether this is true or not, but we feel that in the case of the larger antelope at any rate, which under present conditions exist mainly by the grace of the farmer, strengthened by the deterrent effect of the game laws, the populations reflected by our figures represent a safe minimum, perhaps not too far removed from the maximum.

In the case of species for which only "percentage occurrence" was calculated, the most interesting aspect to emerge is their relative status and distribution. All these figures are not to be taken too seriously: they are intended to give only a rough idea of the position.

(b) Conservation Aspects

The following ungulates, known to have occurred in some parts at least of the Cape Province in historic times, are now extinct: White Rhinoceros, Burchell's Zebra, Quagga, Hippopotamus, Giraffe, Red Duiker (? see Sclater, 1900, Vol. 1 p. 162), Roan Antelope, Blaauwbok and Tsessebe.

A few other species were extinct but have been re-introduced on a small scale. Black Rhinoceros (a pair) have recently been brought into the Addo National Park. (Note: As this paper is being revised for publication we learn that the Hippopotamus has now also been re-introduced into the Addo Park). Black Wildebeest are presently found, according to our questionnaires, on two farms in each of the Divisions of Kimberley and Herbert and on one farm in each of those of Gordonia (doubtful, probably Blue Wildebeest is meant), Philipstown and Bedford. They have also been released in the Mountain Zebra National Park, Cradock. When Bigalke (1947) carried out his survey of the species he found only three herds in the Cape Province. The largest of these, on De Beers Company property near Kimberley, has not been included by us since most of the land concerned is in fact situated in the Orange-Free State. One of the remaining two was in the enclosures at Groote Schuur (Cape Town), where these animals still occur, while the other was on a farm in the Graaff Reinet Division. We received no record from here. It is pleasing to note the improvement, slight though it is, in the status of the Black Wildebeest since 1947.

The third re-introduced species is the Impala, of which we have the following records: Kimberley (1 farm, 25 head), Herbert (1 farm, 4 head), Philipstown (1 farm, 9 head). All of these occurrences are outside the original range of Impala which, in historical times, do not appear to have come much further south than the vicinity of Kuruman. It is likely that Blesbok were also at one time extinct in the Province, since the majority of extant herds stem from introductions, but proof one way or the other is almost impossible to obtain. The species is now widespread (Map XI).

Some non-indigenous forms have also been introduced, viz. Inyala and Lechwe (one farm in the Adelaide Division) and Fallow Deer (in eight Divisions). Red, Sambar and Spotted Deer also occur in the Western Cape but not in the area surveyed.

Our results show that several species have become exceedingly scarce. In the Eastern Province this applies to Oribi in particular, (Table 2), a fact already stressed by Skead (1953). The same holds for Reedbuck for which, although it was not listed on the questionnaires, we obtained the following records: East London, 2 farms one with 4, the other an unspecified

number; Komga, 5 farms, one with 5, one with 3 and three with unspecified numbers.

Mountain Zebra (Table 2) and Bontebok were not dealt with specifically in our survey but they should be mentioned as being amongst the very rare forms. We think we have "discovered" a new herd of Mountain Zebra for we have a record from Adelaide of which Skead (1956) was apparently not aware. Hartebeest (Tables 2 and 3) have long been extinct in much of the Province and it is alarming to see how unsatisfactory their status has become in the Northern Cape. Our estimate of 1060 is nonetheless much higher than that of Rand (1955) who used a different method to arrive at a figure of 350 for the entire Province.

Other species which are very rare indeed on farmed land are Gemsbok and Eland (Table 2) and Blue Wildebeest. None of them were listed on our forms so that some herds may well have been missed, but the position revealed by our results is disappointing. Population estimates obtained are: *Gemsbok*—Kimberley, 1 farm, 20; Herbert, 2 farms, 10; Postmasburg, 1 farm, 1; Hay, 3 farms, 8; Kuruman, 4 farms, 23+; Gordonia, 8 farms, 809; Total 871. *Eland*—Kimberley, 2 farms, 4+; Herbert, 1 farm, 6; Postmasburg, 3 farms, 23; Hay, 2 farms, 8; Barkly West, 1 farm, 5; Kuruman, 1 farm, 14; Vryburg, 1 farm, 16; Gordonia, 3 farms, 20; Philipstown, 1 farm, 4; Total 100. In most if not all cases the animals were obtained elsewhere and introduced by farmers. *Blue Wildebeest*—One landowner in the Kuruman Division recorded 2 while another stated that they sometimes trekked onto his property. It would seem that this antelope is practically extinct on farmed land in the Cape.

Hartebeest, Gemsbok, Eland and Blue Wildebeest are found in considerable numbers in the Kalahari Gemsbok National Park and sporadic mass movements sometimes bring large herds from the Bechuanaland Protectorate over the Molopo River into the Gordonia, Kuruman and Vryburg Divisions (see e.g. Cape Nature Conservation Report, 1958). These animals are however merely transient visitors.

Of the three antelope restricted largely to high country, the Klipspringer is the least abundant. Our population estimate of 3810 suggests that it is in some danger of extinction. Rand (*op. cit.*) gives a figure of 6,550 for the entire Province. For Vaal and Rooi Ribbok, on the other hand, our totals of 9,950 (Rand: 5,970) and 19,268 (Rand: 3,755) respectively are surprisingly high.

The Kudu is unique among the larger antelope for there is good evidence that its range is increasing and it is now found in parts from which it has long been absent. This has also been remarked by Skead (1958). In view of the animal's quite well marked preference for heavily bushed, rocky country it can only be expected in a few Divisions but within these the percentage occurrence has proved to be generally high, especially in the South-West (Map X).

Blesbok are reported from 42 of the 55 Divisions and the total population estimate of 8,890 is very much higher than that of Rand (*op. cit.*, 2,138 for the whole Province). Although the percentage occurrence is nowhere very great, the status of the species is quite satisfactory when one considers that most of the herds arise from introduced stock. The animal is widely available for sale, indeed it is now almost a beast of commerce, and one can confidently predict an upward trend in its future status.

The Springbok is the most numerous and widespread medium-sized game animal in the area investigated, with an estimate of not less than 95,833 (Rand: 14,280). Only 12 of the 55 Divisions reported no Springbok, 10 of these also lacking Blesbok; this appears to reflect unsuitable habitat conditions. There is and has been a great deal of Springbok re-stocking, although perhaps not to the same extent as with Blesbok since original stocks of the first-named survived quite widely when farms were settled and fenced.

Duiker and Steenbok enjoy an extensively widespread distribution and a high percentage occurrence. Broadly speaking the same is true of the Antbear and, to the regret of the farming community, of the Dassie, except in flat country. As there are grounds for suspecting a

confusion between Dassie and Tree Dassie ("Bush Baby" of the eastern region of the Province), our data on the latter is rather suspect. It does occur extensively in the eastern region.

The status of Bushbuck, Blue Duiker and Bushpig, within their limited ranges, appears to be satisfactory, but in many Divisions the percentage occurrence of Grysbok is low.

(c) Zoogeographical Aspects

From information obtained in a survey of this nature it is difficult to extract zoogeographical data. For most species of ungulates the main factor influencing occurrence is, and has been for a long time, the human one. Nevertheless in the case of some species, whose elusive habits, or the vegetational or topographical features of the country in which they live, have protected them from extermination, interesting distribution patterns have emerged. They are not new or startling, but serve to confirm more or less objectively our existing ideas, showing a correlation between vegetation and/or topography and distribution, almost in spite of the activity of man.

In the areas studied four species—Bushpig, Grysbok, Blue Duiker and Bushbuck—occur only in the southernmost portion, i.e. the south-eastern Cape. Of the 33 Divisions in which some or all are found, 20 or 21 (the one Aliwal North record is doubtful) have Bushbuck, 24 have Bushpig, 26 have Blue Duiker and 31 have Grysbok. From Maps I, II and III it is clear that Bushpig, Blue Duiker and Bushbuck occupy very similar ranges, being most frequent in the Divisions nearest the coast and dropping off as one moves inland. They are centred about the Divisions in which the vegetation is predominantly Bushveld, Macchia, Forest and Scrub-Forest (Acocks, 1953, Map II) or combinations of these types. Their concentration appears to diminish as the Karoo influence increases and they are absent both in the Karoo proper and further north. Although Bushpig is also recorded in the Vryburg Division, this must be treated with reserve. Two farmers wrote "Bosvark" on their forms, one of them also adding "Vlakvark" (Warthog). It seems highly unlikely that Bushpig would live in the environment provided by the Vryburg Division. Warthog are found in the Kalahari Gemsbok Park further west and may thus conceivably also be present in Vryburg but the question needs further investigation.

In the case of Grysbok (Map IV) the pattern is similar to that shown by Bushpig, Blue Duiker and Bushbuck but another centre of distribution is revealed by the survey, viz. the north-eastern corner of our area (Divisions of Herschel, Maclear, Barkly East and four adjacent ones). Here the vegetation is Scrubby Mixed Grassveld and Mixed Grassveld (Acocks, *op. cit.*) and high mountains with sheltered valleys predominate. Apparently this country is ecologically suitable for Grysbok—they are probably restricted to the valleys—but not for the other three "south-eastern" species.

Map V illustrates the rather neat distribution pattern of the Duiker. The survey showed it to have the highest percentage occurrence in the extreme south (Bushveld, Macchia, Forest and Scrub Forest and related types) and in the extreme north (Bushveld), i.e. in areas with good cover. In the predominantly Karoo Divisions it proved to be rare and no records were forthcoming from Hanover. It also appears to be absent in five mountainous Divisions (Burgersdorp, Lady Grey, Barkly East, Maclear and Dordrecht).

These findings indicate that while cover in the form of dense vegetation is a habitat requirement common to Bushpig, Blue Duiker, Bushbuck, Grysbok and Duiker, the last named tolerates a wider range of environmental conditions. It is widespread in the dry bush country of the northern Cape where the other four species are absent.

The distribution of the Springbok is more subject to the influence of man than that of the preceding forms, since it can be freely bought and is often used for restocking. Nevertheless the survey shows a largely "natural" pattern (Map VI). As one would expect of a typical plains animal, the highest percentage occurrence is in the Karoo Divisions and falls off to

the south and east and to the north. From most of the densely bushed coastal Divisions and from some of those in high mountainous country no records were obtained. North of the Orange River we suspect human influence to have been more important than elsewhere in accounting for the quite low percentage occurrence. Since Springbok are numerous in the Kalahari Gemsbok National Park at present it seems likely that they were equally common in the similar country of the northern Divisions in the past. Much of the land presently farmed in Gordonia, Kuruman and Vryburg has only been settled comparatively recently and while it was unoccupied crown land illicit hunting decimated the fauna.

Vaal and Rooi Ribbok (Maps VII and VIII) show a distribution in conformity with their preference for hilly terrain. On the whole they were reported most frequently from the most mountainous Divisions. Similarly Klipspringer (Map IX) records came mostly from mountainous areas or from hilly parts of otherwise flat country, e.g. the Langeberg and Korannaberg ranges and the Kuruman Hills in the Divisions of Postmasburg, Kuruman and Hay and the koppies along the Orange River in Gordonia.

Kudu, lovers of thick cover, ideally, it would seem, in combination with rocky hills, are centred around two parts of the country surveyed, the south-west and the north. In the south-west (Map X) koppies or thick bush, or both, predominate and the percentage occurrence is high. In the north suitable habitat occupies a relatively small percentage of the total area, e.g. in the northern Cape Kudu are more or less confined to the Vaal and Orange Rivers, the flanks of the Ghaap Plateau and the Langebergen. The percentage occurrence is consequently lower.

We have mapped the Blesbok records (Map XI) mainly for the sake of showing where they are now found and not from zoogeographical considerations. As has already been pointed out, practically all present occurrences are the result of restocking.

The ubiquitous forms—Antbear, Steenbok and Dassie—have not been mapped. In the case of the latter, Table 3 shows that it is very rare or absent in the flat Kalahari country of the northern Cape. The remaining species dealt with in this survey are now so rare that they are of little zoogeographical interest.

We are left with animals not mentioned in the questionnaires but which must be touched on for the sake of completeness. The Elephant, formerly very widespread over the Province, is now of course restricted to the Knysna Forests and the Addo National Park while the Buffalo remains in the last-named sanctuary only. The Bontebok, always with a restricted range, has been adequately dealt with in the literature (Bigalke, 1955 and Skead, 1958).

It is apposite to note here an old record, mentioned by Sclater (1900) but apparently since forgotten. Burchell (1822), who was very well aware of the difference between Quagga, Zebra and Mountain Zebra, wrote that he saw a herd of Mountain Zebra at Kosi Fountain. This is now called Khosis and is situated in the Ghatlosi Native Reserve, Kuruman Division. In his entry for July 2nd, 1812, he also says "The dauw, or 'mountain horse', inhabits, as I was informed, the Kamhanni Mountains", now the Kuruman Hills. If his observation is correct there must have been an interesting population of *Equus zebra*, isolated from others of this species by hundreds of miles of flat country.

The occurrence of three ungulates, now extinct in the Province (Impala have been re-introduced), in historical times, is of some zoogeographical interest. The Impala (Barrow, 1806, Lichtenstein, 1812, Burchell, 1822 and Thompson, 1827) was quite common in the vicinity of Kuruman. The Tsessebe was described by Burchell from the same area, having previously been encountered there by Truter and Somerville (see Sclater, 1900. Vol. 1 p. 146) while Cumming (1850) saw it in what is now the Division of Herbert. Truter and Somerville (Barrow, 1806) found Roan Antelope near Kuruman and Cumming (*op. cit.*) shot one on the west bank of the Vaal, near the present village of Campbell in the Herbert Division. All three must have been at the south-western limit of their range when in the northern Cape

and a zoogeographical investigation of this area might well reveal some interesting data on tropical or sub-tropical intrusive forms.

SUMMARY

The results of a questionnaire survey of ungulate mammals on farms in 55 Divisions in the eastern and northern parts of the Cape Province are reported. 11,824 forms were sent out and 3,057 (25.9%) were completed and returned by farmers. Population estimates were obtained for Oribi (121), Klipspringer (3,810), Vaal Ribbok (9,950), Rooi Ribbok (19,268), Springbok (95,833), Blesbok (8,890), Red Hartebeest (1,060) and Black Wildebeest (34). The occurrence of another ten species was studied while farmers supplied data on several additional species not listed on the questionnaires. The method of interpreting the results of the survey is given and it is pointed out that both population estimates and percentage occurrence are not claimed to give anything more than a rough idea of status and distribution. The results are discussed from the points of view of conservation and of zoogeography.

ACKNOWLEDGEMENTS

The authors wish to acknowledge their indebtedness to the numerous farmers who co-operated by returning completed questionnaire forms, often with much valuable additional information; also to members of the staffs of the Kaffrarian and McGregor Museums for the part they played in preparing and distributing the forms. One of us (R.C.B.) is particularly indebted to Messrs. De Beers Consolidated Mines Ltd. for duplicating questionnaires; to Mr. D. Hallam and Miss B. Rees of the Company's Geology Department for assistance with mapping; and to Mr. G. P. Grobbelaar for handling most of the questionnaires.

DISCUSSION.

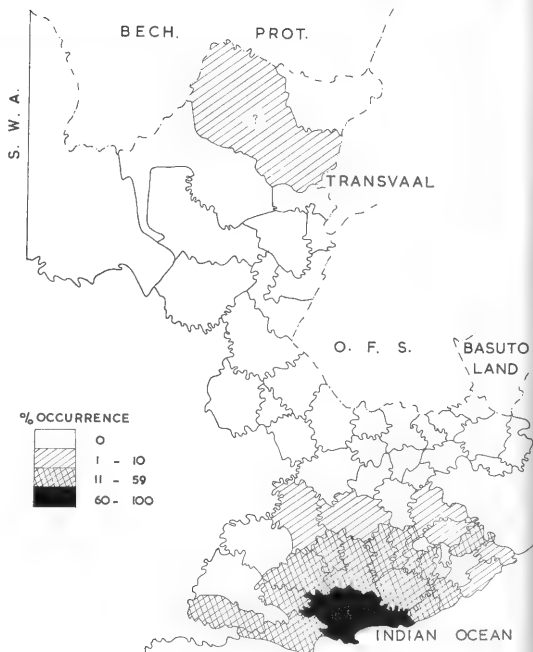
- Dr. Pringle:* Having also had experience of questionnaire surveys, I agree with Dr. Bigalke that figures obtained in this way should not be taken too seriously. For instance, I realized about 10 years ago that Oribi might be nearing extinction in the Eastern Cape and made a personal census, obtaining a count of 51 animals as against your figure of 121. As regards the Kuruman area which has interested so many of the speakers, old records indicate that although there were no wells, people were able to travel freely through the district in historical times because there was plenty of surface water. I would suggest that the area has become very much drier within the last 150 years.
- Dr. Stuckenberg:* Distribution in historical times is best studied in relation to the former distribution of vegetation and for this purpose I have found Acock's Map No. 1 very helpful.
- Dr. Talbot:* Has Dr. Bigalke tried to establish how close farmers' estimates are?
- Dr. Bigalke:* Yes. The general tendency seems to be to overestimate numbers in species regarded as pests; but the larger ungulates are nowadays carefully looked after by conservation-conscious landowners, and estimates for these species are usually reasonably accurate.
- Dr. Winterbottom:* With regard to the numerical increase and extended range of the Kudu, is it possible that this animal may be filling an ecological niche left vacant by other species which have been shot out?
- Dr. Bigalke:* Yes; but it is also possible that it is the result of growing bush encroachment.
- Mr. Skead:* The Kudu influx has occurred in areas which they used to occupy in historic times and it is my impression that they are simply returning to the places from which they were previously driven away or exterminated.

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- Mr. Liversidge:* In South West Africa a similar increase amongst Kudu has been attributed to the increased number of water holes now available.
- Dr. Bigalke:* This is possible, of course, but Kudu are able to survive in waterless areas.
- Mr. Attwell:* Is it possible that in the case of Vaal and Rooi Ribbok Gause's principle may be operating?
- Dr. Stuckenberg:* Does fencing, by preventing natural movements, play a part?
- Mr. Skead:* Ribbok can easily jump fences.
- Dr. Pringle:* And so can Kudu; but jackal-proof netting may be a factor affecting smaller species, especially in the Karoo.

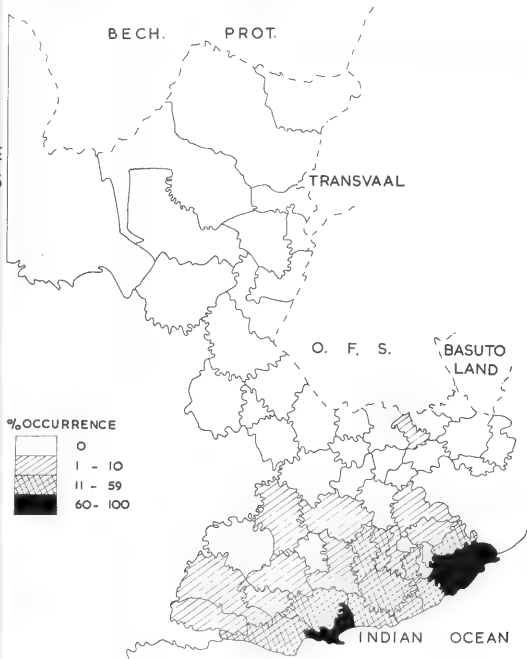
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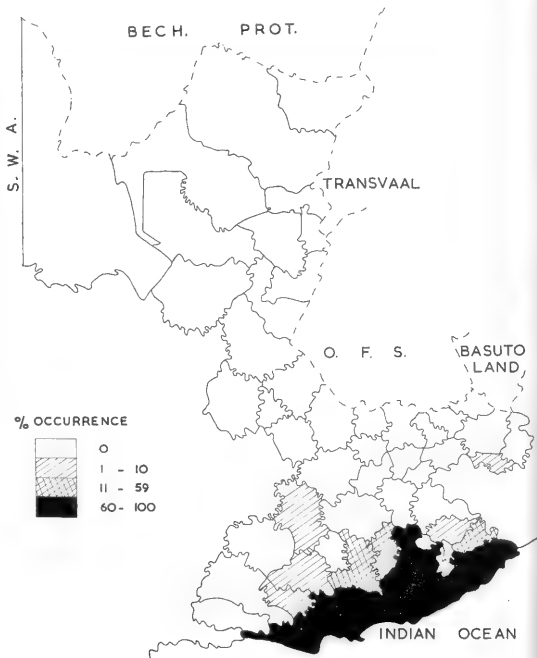


Map I. Distribution of Bushpig based on "Percentage Occurrence".

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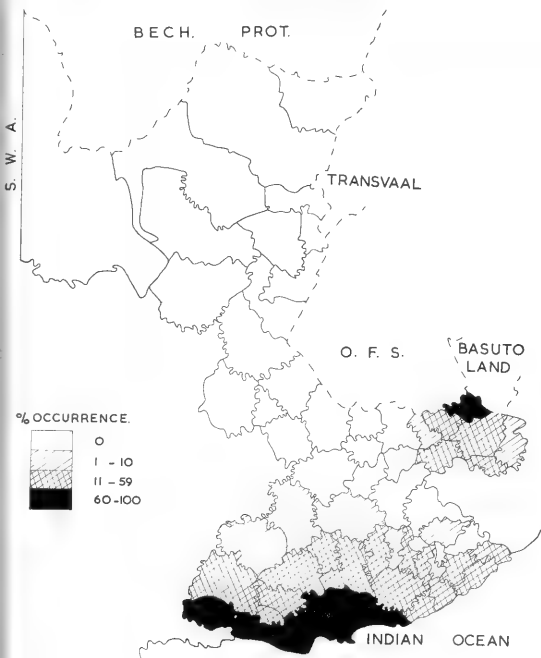


Map II. Distribution of Blue Duiker based on "Percentage Occurrence".

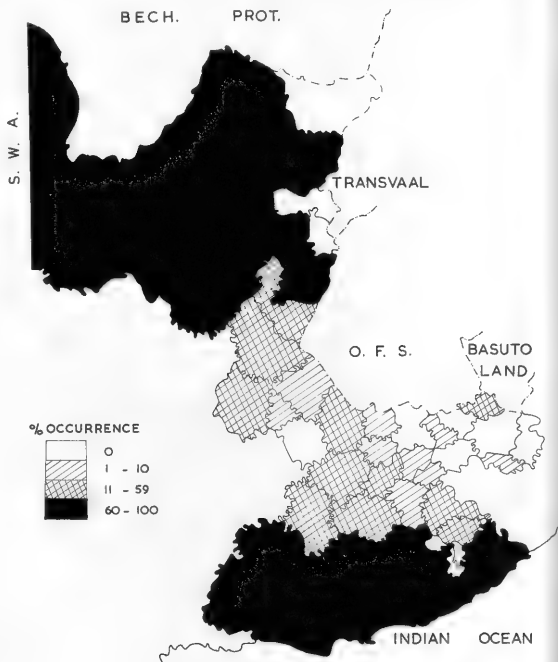


Map III. Distribution of Bushbuck based on "Percentage Occurrence"

STATUS AND DISTRIBUTION OF CAPE UNGULATES, SOUTH AFRICA

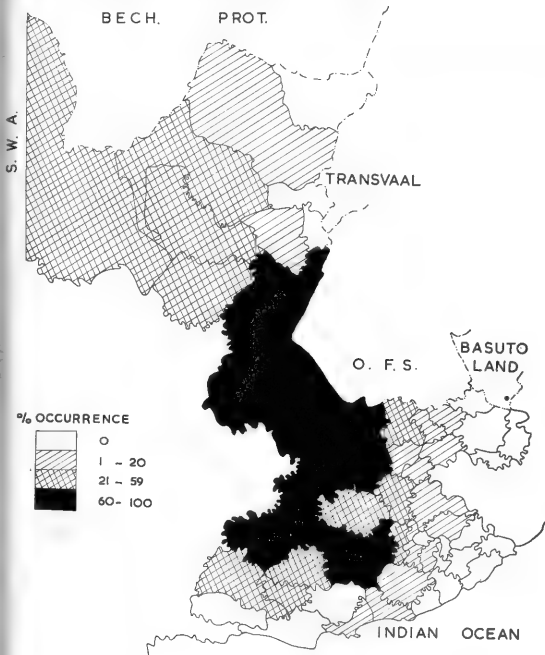


Map IV. Distribution of Grysbok based on "Percentage Occurrence"

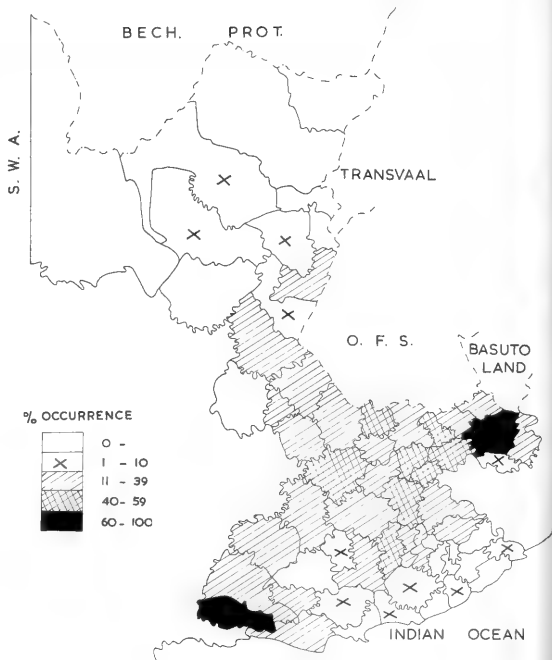


Map V. Distribution of Duiker based on "Percentage Occurrence"

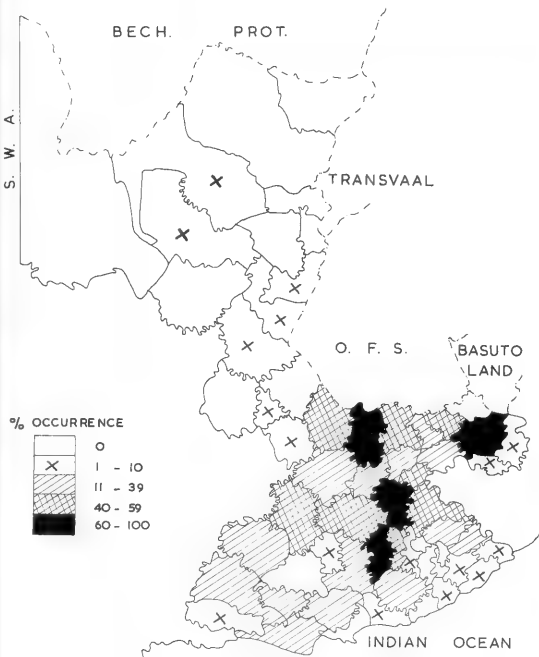
STATUS AND DISTRIBUTION OF CAPE UNGULATES, SOUTH AFRICA



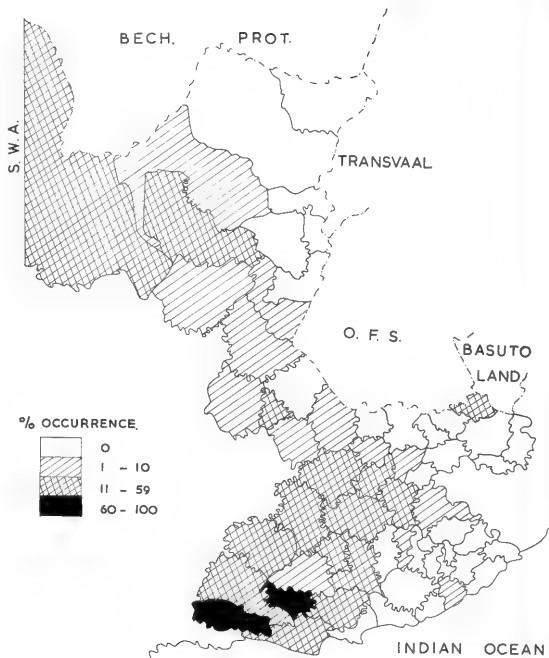
Map VI. Distribution of Springbok based on "Percentage Occurrence"



Map VII. Distribution of Vaal Ribbok based on "Percentage Occurrence"

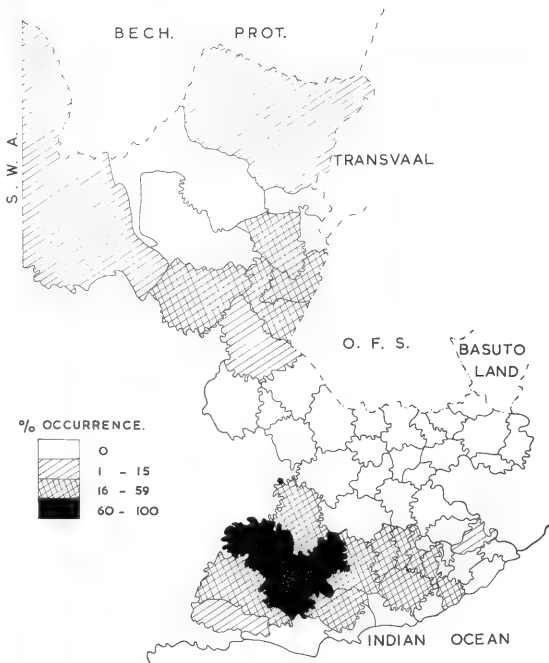


Map VIII. Distribution of Rooi Ribbok based on "Percentage Occurrence"

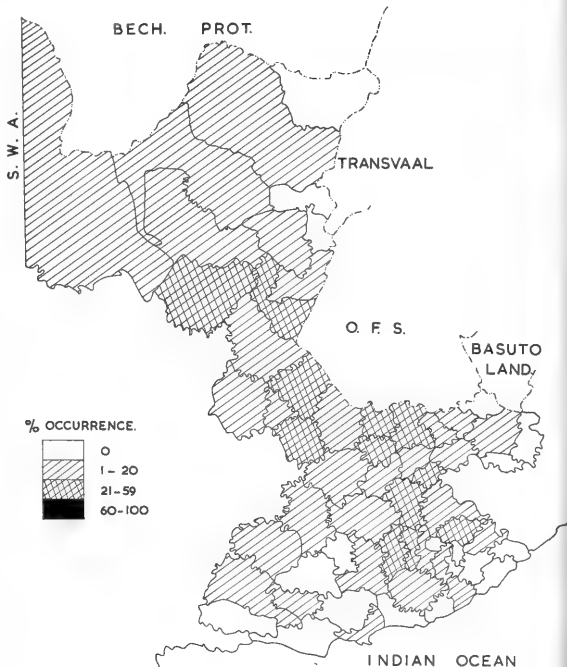


Map IX Distribution of Klipspringer based on "Percentage Occurrence"

STATUS AND DISTRIBUTION OF CAPE UNGULATES, SOUTH AFRICA



Map X Distribution of Kudu based on "Percentage Occurrence"



Map XI Distribution of Blesbok based on "Percentage Occurrence"

STATUS AND DISTRIBUTION OF CAPE UNGULATES, SOUTH AFRICA



Key Map. Showing names of Divisions, abbreviated as in Table 3. Divisions without names were not included in the survey.

J. VINCENT

DIRECTOR OF WILD LIFE
CONSERVATION IN NATAL.

The distribution
of ungulates
in Natal

Although it is not difficult to describe the present day distribution of each species of ungulate mammal in Natal, it is hard even to guess at the distribution of most of the same animals prior to the closing years of the 19th century. Early explorers, travellers and hunters often gave us good accounts and lists of the wild life met with on their wanderings in southern Africa, but it is noteworthy that virtually all of these people skirted the borders of Natal, doubtless because of the dissident nature of its Bantu population. As a result, prolonged research among bookshelves of "Africana" reveals little if anything in the way of information about the wild life found in Natal before permanent European settlement.

It is manifestly true also to say that long before white settlement can have had any material effect upon the populations of indigenous fauna, they must have been very extensively changed by the dense population of those great hunters, the Zulus. It is indubitably the case, in fact, that because of close settlement by these Bantu people, over a long period before the advent of the European, we shall never know the true details of mammal distribution in Natal prior to its wide alteration by human influences.

Another important and undoubtedly pertinent aspect of the problem is that settlement by man has for long inhibited any seasonal movements, particularly by the larger mammals, from the lowveld to the midlands or highveld. It is well known that the grasslands of the midlands and sourveld areas of Natal have a negligible carrying capacity for livestock during the long autumn and winter months; also that farmers there experience great hardship and expense in maintaining their animals in any sort of condition during that time. It is also well known that the farmers who do make and have made substantial incomes are those who own both a lowveld and a highveld farm, and are able to move their cattle from the former to the latter with the advent of spring, and *vice versa* in early autumn. Indubitably the same types of movements were carried out by many ungulates, although for many generations now they have been unable to follow any such age-old custom.

There are two species which at the present time are found only at high altitudes on the face of the Drakensberg massif, and it is very probable that they have always been thus localized. They are the Vaal Ribbok or Grey Rhebuck *Pelea capreolus*, and an as yet unidentified race of the Klipspringer *Oreotragus oreotragus*; the latter seldom occurring below 8,000 ft., and the former seldom below 4,500 ft. a.s.l.

Others among the ungulates found in the sourveld country no doubt in the past ranged or were distributed widely over the midlands and highlands, whereas now they are confined

to the fastnesses of the Drakensberg, to a few areas of particularly suitable habitat, or to the vicinity of extensive private properties where they have for a long time been rigorously preserved. These are the Tree Hyrax *Dendrohyrax arboreus*, Eland *Taurotragus oryx*, the Mountain Reedbuck *Redunca fulvorufa* and the Oribi *Ourebia ourebia*.

In so far as the largest ungulates are concerned, and those incompatible with organized agriculture, or previously much persecuted, it can be said that at the present time they are entirely confined to the larger, proclaimed game reserves in Zululand or to their near vicinity. In this group come the African Elephant *Loxodonta africana*, Black Rhinoceros *Diceros bicornis*, Square-lipped Rhinoceros *Ceratotherium simum*, Burchell's Zebra *Equus burchelli*, Brindled Gnu [or Blue Wildebeest] *Connochaetes taurinus* and, apparently, the Warthog *Phacochoerus aethiopicus*.

The smaller ungulates, which are either difficult to hunt, not prized for their flesh or skin, or to all intents and purposes harmless to agricultural interests, do survive in adequate numbers for some better light to be thrown upon their general distribution within the Province. Quite naturally a few of these are ubiquitous in suitable vegetation and terrain; such as the Rock Hyrax *Procavia capensis*, Grey Duiker *Sylvicapra grimmia*, Reedbuck *Redunca arundinum* and Bushbuck *Tragelaphus scriptus*. It is perhaps possible here also to include the Bushpig *Potamochoerus porcus*, although its range has been much reduced and now may be restricted to the lowest levels.

Generally speaking, however, the distribution of the others seems to adhere closely, in the same way as does that of many bird species, to the acacia thornveld. The result is an extensive distribution at the lowest altitudes, from sea level to about 1,500 ft., with some considerable westward extensions of range, reaching even to slightly higher altitudes up into the deeper valleys of such river systems as the Tugela and Umfolozi. As in the birds it is this lowest altitudinal zone which contains the largest number of species. Those ungulates whose main populations can be included here are the Hippopotamus *Hippopotamus amphibius*, Red Duiker *Cephalophus natalensis*, Steenbok *Raphicerus campestris*, Impala *Aepyceros melampus*, Kudu *Tragelaphus strepsiceros*, and African Buffalo *Syncerus caffer*.

Also to be included among these lowveld species it is interesting to note at least three species, the Suni *Nesotragus moschatus*, Waterbuck *Kobus ellipsiprymnus* and Inyala *Tragelaphus angasi*, which illustrate that same intrusion of tropical forms as is found among the avifauna, extending from the Moçambique border to the St. Lucia area, or to about the mouth of the Umfolozi river system. In earlier times the intrusion perhaps extended even a little farther south along the littoral, perhaps to the area of the Tugela River mouth.

There is one other species not yet mentioned, which it is perhaps not entirely accurate to list among the lowveld forms, and this is the Blue Duiker *Cephalophus monticola*. Although commonest at the lowest levels, it is really an animal of evergreen indigenous cover, whether this be coastal jungle or rain forest. Accordingly it still extends into most of those relict patches of rain forest which occur widely in the midlands, and there it may be found up to about 4,000 feet a.s.l.

During this brief overall survey of the various habitats, twenty-seven of the thirty-one ungulates have been mentioned. The four which remain fall into entirely different categories.

One of them is the Grysbok *Raphicerus melanotis*, and this is best listed as an at present unidentified probability. There is certainly a small red antelope in forest patches in deep valleys of the high Drakensberg, and the remains of a carcass seen showed some traces of white hairs. It seems likely that either an undescribed, high altitude race of *R. melanotis* is involved, or possibly of *R. sharpei*.

The remaining three mammals in Natal's ungulate list are best described merely as recent reintroductions. The indigenous race of the Red Hartebeest *Alcelaphus buselaphus* seems now to be extinct in Natal. Little more need be said about it here because the whole subject has

been adequately covered in an excellent paper on the animal's disappearance, which appeared in the May 1961 issue (Vol. 2, No. 2) of *Natal Wild Life*. It is included in this present review of the distribution of ungulates in Natal, merely in order to record that 1960 saw the Natal Parks, Game and Fish Preservation Board's first attempt to reintroduce the species. During that year two juvenile animals were obtained from De Beers Consolidated Mines, at Kimberley, and placed at the Giants Castle Game Reserve where they are now doing well. It is hoped that further animals may later be added to this small beginning.

This leaves only the Giraffe *Giraffa camelopardalis* and the White-tailed Gnu [or Black Wildebeest] *Connochaetes gnou*. It has not been possible conclusively to determine whether giraffes did in fact once occur in Zululand, but the habitat was so obviously suitable for them that giraffes were introduced in 1947 and 1950 into the Hluhluwe Game Reserve, where a small party now breeds and thrives. The White-tailed Gnu is another species concerning whose earlier occurrence in the highveld areas of Natal little if anything can be gleaned from old literature. That the animal did occur here seems to be clear enough, and it is perhaps pertinent that two of them grace the Province's coat of arms.

In any event two large reserves in the Drakensberg controlled by the Natal Parks, Game and Fish Preservation Board—the Giants Castle Game Reserve and the Royal Natal National Park—contain ample grass cover to carry a population of gnus without any detrimental effects upon the essentially browsing population of eland. The Board accordingly decided upon a reintroduction of the species and it was in 1956 that the first few animals were obtained. More were added during 1957 and again in 1958, with the result that the new population now numbers thirty-four individuals which can happily be said to be thriving in every sense of the word.

A slightly more detailed summary of the distribution of each individual species listed in systematic order, is as follows:

1. African Elephant *Loxodonta africana*.

Limited to a small herd on the eastern boundary of the Ndumu Game Reserve, adjacent to the Mozambique border.

2. Rock Hyrax *Procavia capensis*

General throughout the Province in suitably rocky habitat.

3. Tree Hyrax *Dendrohyrax arboreus*

Recorded in the large Karkloof Forest of the Natal midlands and doubtless occurs in other evergreen rain forests of the Province; but no records can be traced and little seems to be known of its incidence or distribution.

4. Black Rhinoceros *Diceros bicornis*

Confined to the game reserves of Mkuzi, Hluhluwe and Umfolozi; also found in the State-owned lands between the two latter, known as 'The Corridor'.

5. Square-lipped Rhinoceros *Ceratotherium simum*

Confined to the Hluhluwe and Umfolozi Game Reserves in north-eastern Zululand. (A wide knowledge of the different field habits and habitats of the two rhinos, as well as of their utterly dissimilar characteristics and reactions, makes it impossible for the writer to agree with those who treat them as congeneric).

6. Burchell's Zebra *Equus burchelli*

Confined to the game reserves of Mkuzi, Hluhluwe and Umfolozi and the State-owned land between the two latter. (According to Ellerman, Morrison-Scott and Hayman the Natal animal is called Chapman's Zebra *E. b. antiquorum*. The writer, however, prefers to retain the name Burchell's for the trivial term, since he is by no means happy about Zululand and Transvaal examples being considered one and the same. The two are always easy to recognize in the field because of their distinctive leg striping).

7. Bushpig *Potamochoerus porcus*

Widespread and general throughout the littoral, but apparently not found much above 1,000 to 1,500 ft. a.s.l. Occurs in some evergreen forests, but nowadays mainly confined to sugar cane lands, wherein it is increasingly common.

8. Warthog *Phacochoerus aethiopicus*

Apparently now restricted to the game reserves of Mkuzi, Hluhluwe and Umfolozi, and the adjacent State-owned lands.

9. Hippopotamus *Hippopotamus amphibius*

Confined to a few waterways of the north-eastern Zululand littoral, from the Moçambique border south to about Richards Bay. More detailed localities are—the Ndumu Game Reserve and adjacent Pongolo River, the Pongolo lakes, the Kosi Bay lakes, Lake Sibayi, the St. Lucia lake system and its tributaries, the lower Umfolozi River and Lakes Eteza and Umsingazi.

10. Giraffe *Giraffa camelopardalis*.

Only in the Hluhluwe Game Reserve, where introduced.

11. Red Duiker *Cephalophus natalensis*

In thick coastal scrub and evergreen forest patches of north-eastern Zululand, also in some gullies of the Lebombo hills; but not extending much above 1,000 ft. a.s.l. Although widespread it is nowhere common. The type locality is near Durban, and doubtless it was formerly widespread in the coastal bushes of southern Natal. At the present time, however, it would seem to have disappeared from the area, except for a few individuals in a well preserved forest in the magisterial division of Inanda.

12. Blue Duiker *Cephalophus monticola*

In suitable evergreen thickets and forest throughout Natal as far north as about the Umfolozi River system. Mainly in the coastal areas, but also in suitable indigenous rain forest of the midlands up to about 4,000 ft. a.s.l.

13. Grey Duiker *Sylvicapra grimmia*

Quite ubiquitous and general at altitudes up to about 6,000 ft. in the foothills of the Drakensberg. Extremely common in the game and nature reserves. Seems to be the only antelope which survives even in some Native reserves.

14. Steenbok *Raphicerus campestris*

Essentially an animal of the drier and more open types of lowveld. Occurs commonly in the Umfolozi Game Reserve and probably now no farther south. It is also in the Mkuzi Game Reserve and less commonly, although widespread, from the Hluhluwe Game Reserve northwards into the Ngotshe district and throughout north-eastern Zululand. (It is not known whether the subspecies involved is *capricornensis* or *zuluensis*. The writer has also recorded no Steenbok from the highveld, and not only doubts its occurrence there but also knows nothing of the so-called race *natalensis*, described as from "Drakensberg, Natal.")

15. Grysbok *Raphicerus melanotis*

Whether this occurs at all in Natal is open to doubt. No specimen has definitely been recorded in the Province, certainly not for a very long time, and even if the skulls in the British Museum, reputed to be of this species and from Zululand, do emanate thence it has not been seen in any of the Zululand game reserves. A few examples of a small, unidentified antelope do still exist in high forest patches on the slopes of the Quathlamba Drakensberg, and it is possible that these may represent some race of the Grysbok, but none has yet been obtained for identification.

16. Oribi *Ourebia ourebi*

Nowhere particularly common, except perhaps in the Giants Castle Game Reserve and on one or two highveld farms where wild life is strictly preserved. Nevertheless still occurs throughout the Province in suitable areas of open grassveld, particularly in the Natal midlands from about 7,000 ft. down to about 1,500 ft. a.s.l. The distribution or incidence is really now governed by the degree of protection afforded. Without doubt the species was formerly much more widespread.

17. Suni *Nesotragus moschatus*

In suitably dense coastal bush east of the Lebombo range and from the Moçambique border south to about St. Lucia. Commonly seen in the game reserves of Mkuzi and Ndumu.

18. Klipspringer *Oreotragus oreotragus*

Now rare and apparently found only in the Umfolozi Game Reserve and at one or two points farther north in the Lebombo range. Also found sparingly above 8,000 ft. and in suitably guarded areas, on the steep rocky faces of the Quathlamba Drakensberg, from Giants Castle to Royal Natal National Park.

19. Grey Rhebuck *Pelea capreolus*

Only found on steep and open, grass covered rocky slopes of the high Drakensberg, from about 8,000 ft. to 4,500 ft. a.s.l.; seldom now found at any lower altitude.

20. Reedbuck *Redunca arundinum*

Ubiquitous throughout the Province and at all levels below about 7,000 ft. Widely distributed but nowhere common.

21. Mountain Reedbuck *Redunca fulvorufula*

Appears to be found sparingly on open, rocky hillsides throughout the Province; although because of the restricted nature of its habitat often heavily poached and disappearing from

THE DISTRIBUTION OF UNGULATES IN NATAL

some areas, particularly at the lower levels. Although nowhere very common, except in the Drakensberg wild life sanctuaries, it is found from about 8,000 ft. where it occurs alongside *Pelea capreolus*, right down to hills in Zululand of no more than 1,500 ft. altitude.

22. Waterbuck *Kobus ellipsiprymnus*

Apparently now confined to the game reserves of Hluhluwe and Umfolozi.

23. Impala *Aepyceros melampus*

Quite widely distributed in the Zululand acacia thornveld north of the Umfolozi River, particularly in the game reserves of Umfolozi and Hluhluwe and in adjacent hills up into the Ubombo and Ngotshe districts. Reintroduced into the St. Lucia and Ndumu areas, and more recently among many privately owned thornveld farms virtually throughout the Province.

24. Red Hartebeest *Alcelaphus buselaphus*

Only in the Giants Castle Game Reserve where introduced.

25. White-tailed Gnu *Connochaetes gnou*

Long disappeared from Natal in a feral state. Reintroduced into the Giants Castle Game Reserve in 1956 and 1957 and into the Royal Natal National Park in 1958.

26. Brindled Gnu *Connochaetes taurinus*

Now restricted to the game reserves of Umfolozi, Hluhluwe and Mkuzi and some closely adjacent State-owned lands.

27. Bushbuck *Tragelaphus scriptus*

Ubiquitous from about 6,000 ft. down to sea level in all suitably dense evergreen cover, whether this be coastal jungle, riverain scrub or mountain rain forest.

28. Inyala *Tragelaphus angasi*

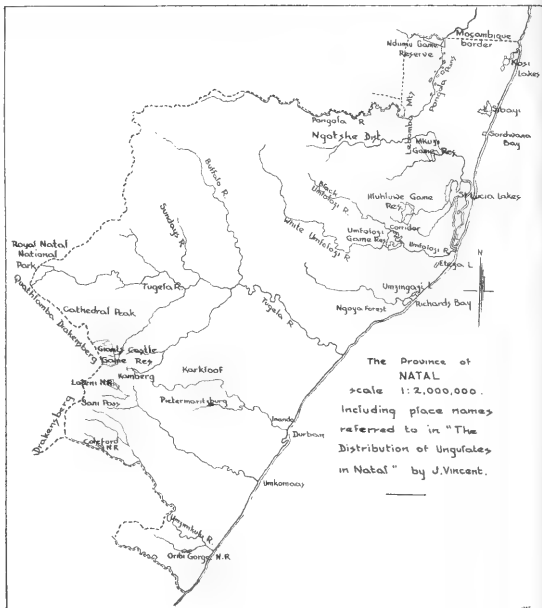
Now limited to the proclaimed reserves of Mkuzi, Hluhluwe, Umfolozi, Ndumu and St. Lucia. Until this century no doubt widely distributed in suitably dense cover to the east of the Lebombo range south to about the Umfolozi River. Ellerman, Morrison-Scott and Hayman say—"introduced into the Hluhluwe Game Reserve", quoting Roberts, but this was a reintroduction from the Mkuzi Game Reserve, into another sanctuary where the species had been common fifty years earlier.

29. Kudu *Tragelaphus strepsiceros*

Common in the game reserves of Mkuzi, Hluhluwe and Umfolozi; also found on some private farms in the divisions of Ubombo and Ngotshe.

30. Eland *Taurotragus oryx*

Only in the Drakensberg and there mainly in the Giants Castle Game Reserve, whence it has extended outwards to a distribution which can be described as—along the eastern face of the Drakensberg from about Sani Pass to Cathedral Peak, and between the 8,000 ft. and 5,500 ft. levels.



31. African Buffalo *Syncerus caffer*

The game reserves of Hluhluwe and Umfolozi and the immediately adjacent State-owned lands. It is likely also that a few animals remain in the vicinity of the Ngoya Forest, near Eshowe.

DISCUSSION

Mr. Grindley: Will there be any attempt to correlate the maps presented for the different provinces?

Prof. Balinsky: Perhaps by the authors themselves, but it is not considered an editorial task.

Dr. Talbot: Apropos of Mr. Van Ee's earlier remarks on exotic ungulates, the Cape Province has a Department of Nature Conservation but several kinds of deer have been introduced.

Mr. Bateman: I have investigated the origins of the deer in this province. It appears that the earliest introduction occurred in the 1870's when a Mr. Ohlsson brought in Red Deer from Scotland. Fallow Deer were imported in the 1890's and spread mainly from Groote Schuur. These introductions thus took place before any Nature Conservation Department existed. Fallow Deer have always been very popular, largely for their aesthetic appeal, but also because they have proved very hardy and adaptable, able to withstand conditions which have wiped out even indigenous and domestic animals. For instance, during a spell of extreme cold in the Cradock area, Springbok, Blesbok and sheep succumbed while Fallow Deer survived. The danger from the conservation point of view is thus that these introduced forms will spread and multiply at the expense of the indigenous fauna.

Dr. Stuckenberg: On a visit to Madagascar, Fallow Deer were the first animals I saw in the tropical rain forest!

Mr. van Ee: I understand that certain farmers have obtained permits at the present time to introduce another exotic into the Cape, namely Barbary Sheep. Does Dr. Bigalke know whether this is correct?

Dr. Bigalke: I do not know, but if it is so, it is a sad reflection on the responsible authorities.

W. K. KETTLITZ

TRANSVAAL DEPARTMENT OF
NATURE CONSERVATION,
PRETORIA.

The distribution
of some of the larger
game mammals
in the Transvaal
(excluding the
Kruger National Park)

Most of the Transvaal has been surveyed and divided into separate farms, the majority of which are ring-fenced. Probably, therefore, the old migrations of game have stopped. In some places, the natural game has disappeared and a slow process of restocking is now taking place, especially with Blesbok and Springbok, and to a lesser degree with Impala, Blue Wildebeest, Zebra and Black Wildebeest.

It cannot yet be established what the effect on numbers and density of certain species will be after the total fencing of the western boundary of the Kruger National Park. The full effect of this and of the subsequent fencing of the privately owned Sabi Sand Wildtuin and the Timbivati Game Reserve will be apparent within the next few years.

As far as the distribution and present status of mammals in the Kruger National Park is concerned, the student should refer to the Biologist's Report (Anon, 1960), in which a comprehensive summary is to be found.

Where the position of game in the rest of the Transvaal in 1953 is mentioned in this paper, it has direct bearing on a previous survey. (W. K. Kettlitz 1954.)

On the accompanying maps the distribution of herds and, in some cases, the density of the species, or both, is shown. However, no attempt has been made to allocate certain numbers to each symbol on the maps, as it is difficult to do so in all the districts taken together. The actual occurrence of herds, whether small or large gives a clearer idea of distribution than estimates of actual numbers.

BLESBOK

Damaliscus albifrons

The distribution of this species is interesting, as we have its natural habitat with the heaviest population in the south-eastern-districts, with Ermelo as the centre. Numbers gradually diminish towards the south-western districts. This natural distribution is indicated by a line on the map. The herds to the north of that line have been artificially introduced. Thus, during the last ten years the distribution has been extended so that Blesbok are now found in all parts of the Transvaal, but highest densities still remain in the south-eastern districts. This artificial distribution has given new values to the Blesbok. In bushveld and lowveld areas it is expensive to erect fences which will retain popular natural game such as Kudu and Impala. Blesbok, however, can be confined by ordinary fences and seem to thrive in these new surroundings where it was formerly believed they would not survive. This animal is not very selective and is at present not considered to compete with animals which occur naturally.

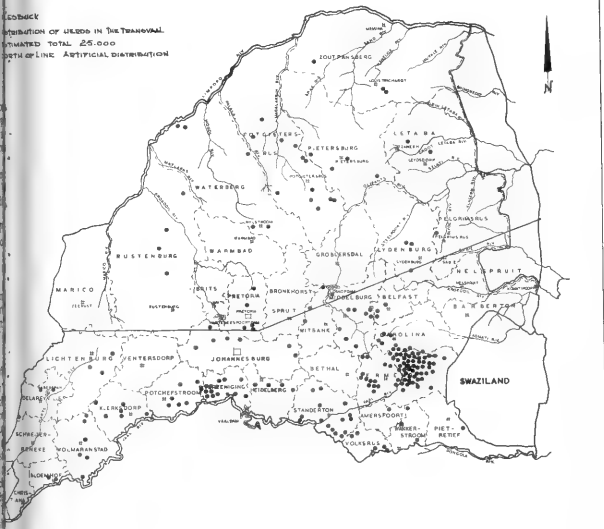
DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

Some conservationists do not agree with the introduction of wild animals into habitats where they do not or did not occur naturally. Where it is uneconomic to re-establish and keep natural species, their preservation depends solely on their aesthetic value and the aims of conservation may be lost. The Blesbok is not an exotic species and its habits are more or less known. Thus, where game is becoming a factor in ordinary farming practice, and because Blesbok can virtually be controlled like other farm stock, the species is very seldom kept for aesthetic purposes only, and its economic value is becoming increasingly prominent.

There are approximately 25,000 Blesbok in the Transvaal and the distribution pattern may be expected to change from time to time as long as it is spread artificially. (Fig. No. 1).

LODBUCK

DISTRIBUTION OF BLESBOK IN THE TRANSVAAL
ESTIMATED TOTAL 25,000
DOTTED LINE ARTIFICIAL DISTRIBUTION



DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

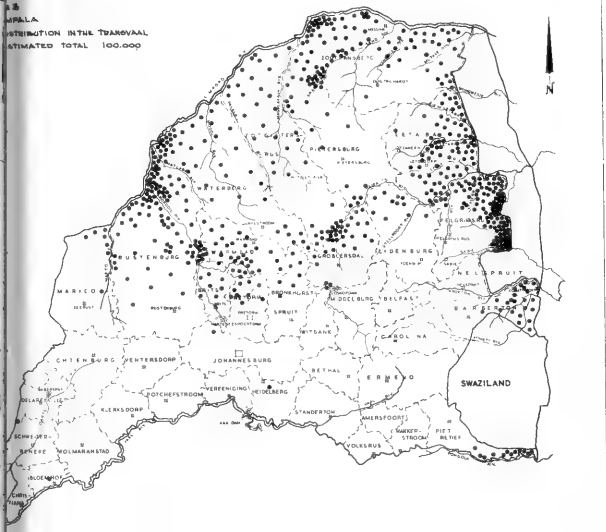
IMPALA

The distribution of Impala in the Transvaal has more or less remained the same as it was in 1953, although densities in some areas have diminished. Places where the populations have decreased considerably during the past ten years are the north-western Limpopo region, areas of the Komatipoort and Pongola (south of Swaziland) and the Klaserie valley in Pilgrim's Rest district. All these have become highly cultivated regions, farms have been subdivided and the game consequently reduced.

Some artificial dissemination has taken place. Introduction into previously unpopulated areas has been achieved with some success. For instance, in the western Transvaal

Aepyceros melampus melampus

IMPALA
DISTRIBUTION IN THE TRANSVAAL
ESTIMATED TOTAL 100,000



where we stocked Impala about ten years ago, they did extremely well and the bloom of the herd has been phenomenal. It was also found in this particular area that competition for feed between Impala and the local species is not heavy as Impala make use of the old diggers' trenches which are not used by the local species. A rough estimate of their numbers in the Transvaal is approximately 100,000. (Fig. No. 3).

BLUE WILDEBEEST

Gorgon taurinus taurinus

The distribution of this species remains much the same as in 1953. Pilgrim's Rest district has the densest population, but numbers are slowly decreasing on account of intensified



DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

farming activities during the past ten years. The species has almost vanished in the Barberton district and numbers are becoming very low in the Rustenburg, Waterberg, Potgietersrust, Soutpansberg and Letaba districts. The "snotsiekte" disease, formerly unknown where cattle and the eastern Wildebeest mixed, has now become a real danger and some ranchers are in favour of exterminating Wildebeest on account of it. A rough estimate of Wildebeest is less than 10,000. (Fig. No. 4).

ZEBRA

Equus burchellii transvaalensis

Distribution remains much as in 1953, with the highest densities in the Pilgrim's Rest,



Letaba and Soutpansberg districts. Where these animals compete with cattle in ranching areas they are slowly being eliminated. The numbers in the western districts are becoming very low. Some introductions in the central Transvaal have taken place. The estimated number in the Transvaal does not exceed 6,000 with less than 1,000 in the western districts. (Fig. No. 5).

KUDU

Strepsiceros strepsiceros strepsiceros

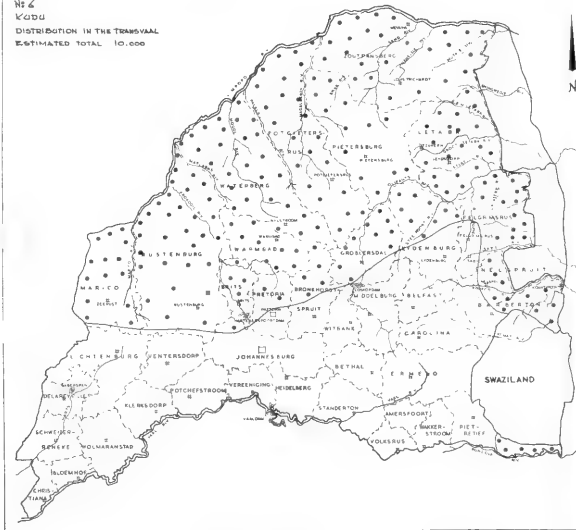
This ungulate is distributed evenly over the whole bushveld and lowveld of the Transvaal. They are most numerous in places where the type of vegetation gives good cover or where they are afforded vigorous protection by owners. In new settlements Kudu do

No. 6

KUDU

DISTRIBUTION IN THE TRANSVAAL

ESTIMATED TOTAL 10,000



DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

much damage to cultivated crops and many of them are destroyed while causing damage. They seem, however, to hold their own against heavy hunting pressure, which may be attributed to their shyness, speed and wonderful camouflage.

They move about so much from farm to farm that it is difficult to estimate numbers. High figures are recorded in game surveys and censuses, but I doubt whether the total reaches the 10,000 mark. (Fig. No. 6).

GREY RHEBUCK (VAALRIJBOK)

Pelea capreolus

This animal is distributed over the central and south-eastern districts of the Transvaal

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GREY RHEBUCK

DISTRIBUTION OF HERDS IN THE TRANSVAAL

ESTIMATED TOTAL 2000



with the heaviest population in the Lydenburg district and the central area where the Waterberg, Warmbaths and Rustenburg districts join. They do not seem to occur in the Soutpansberg range. They are restricted to areas south of the 24th latitude and occur at altitudes above 4,000 ft., preferring the mist belt just above the habitat of the Mountain Reedbuck.

It is hard to establish their numbers but it is estimated that there are not more than 2,000 in the Transvaal. (Fig. No. 7).

MOUNTAIN REEDBUCK (ROOIRIBBOK)

Redunca fulvorufula

This animal is encountered in all regions in the Transvaal where the necessary altitude

NE 8
MOUNTAIN REEDBUCK
DISTRIBUTION OF HERDS IN THE TRANSVAAL
ESTIMATED TOTAL 1400



DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

and ruggedness prevail. The thickest population occurs in the north-eastern highveld with Lydenburg and Middelburg districts as the centre. Their preferred habitat seems to be between 4,000 and 4,500 ft. altitude and some are also found at 3,000 ft. in the Barberton district. The areas just below the mist belt seem to be their favourite haunts. (Fig. No. 8).

WATERBUCK

Kobus ellipsiprymnus ellipsiprymnus

This species occurs in small numbers in the northern part of Marico district. In the Rustenburg district they are found in fair numbers along the rivers, especially so at the confluence of the Marico-Crocodile and at the Matlabas-Crocodile junction. In the



Waterberg and Potgietersrust districts they are scarce. In the Pietersburg district on the Blouberg Private Nature Reserve they are quite numerous and under strict protection. In the Soutpansberg district, especially along the Limpopo, they become more plentiful. The thickest populations occur in the Letaba and Pilgrim's Rest districts where the buck are plentiful on quite a number of farms. Their southern limit is in the Barberton district where they are scarce. There are no Waterbuck in the southern and central Transvaal, except on the Loskopdam Nature Reserve where they were introduced.

It can be stated that there are not less than 2,000 head in the Transvaal. (Fig. No. 9).



ORIBI *Ourebia ourebi ourebi*

The distribution of this animal is more or less in the eastern highveld, the Ermelo district having the highest population. They are also found in the Middelburg, Witbank, Bronkhorstspuit and Pretoria districts. On the farm Uitkomst, close to Krugersdorp, there are about 40 which are kept in a properly fenced reserve and enjoy strict protection. They occur on the grassveld in the Transvaal although it is known that they used to be present in the southern lowveld where they have since disappeared. There are about 750 Oribi in the province. (Fig. No. 10).

ELAND *Taurotragus oryx oryx*

Apart from small herds on the Molongo Flats and in the Shingwedzi area in the north-eastern corner of the Transvaal, there are quite a number of farmers who have small but established herds. In 1953 the estimated number was not more than 75 head. In 1961 the number is well over 100. These herds were all introduced and are settled so that they may be expected to increase at a faster rate than before. The north-eastern herds are the only ones in the natural state. Most of the others are on fenced farms and are treated like domestic animals. (Fig. No. 11).

GEMSBOK *Oryx gazella*

The Gemsbok position is very grave and their total disappearance can hardly be stopped. On the Langjan Nature Reserve they have been steadily decreasing mainly because they were not properly fenced. Several attempts have been made to establish a herd on the S. A. Lombard Nature Reserve without success. Apart from those in zoos, there are only 15 Gemsbok in the Transvaal. (Fig. No. 11).

NYALA *Nyala angasi angasi*

This species is now found in the north-eastern corner of the Transvaal, in the Lydenburg district and on the Loskopdam Nature Reserve. The latter were introduced. The future of those in the wild state is very uncertain. They still do not exceed the 100 mark and are virtually extinct outside the Kruger National Park and Loskopdam Reserve. (Fig. No. 11).

THE RED HARTEBEEST *Alcelaphus caama caama*

The Red Hartbeest is also on the downgrade. A natural herd in the Marico district is slowly declining on account of consecutive droughts over the last few years. There are small herds scattered through the Rustenburg, Waterberg and Potgietersrust districts. The herd on the S. A. Lombard Nature Reserve does not seem to do well. We will, however, endeavour to establish a herd on the Langjan Nature Reserve. The total number in the Transvaal does not exceed 200. (Fig. No. 11).

TSESSEBE *Damaliscus lunatis lunatis*

Tsessebe are still scarce in the Transvaal, and new disease factor has made their future even more doubtful. Since 1953 their numbers have decreased although the distribution remains more or less the same. They are sparsely distributed along the boundary of the Kruger National Park from the Shingwedzi area southwards to the Letaba River. In the Pilgrim's Rest district they are scattered on the farms, Fleur de Lys, Moriah and Buffelshoek having the highest populations. Smaller scattered herds are found in the Waterberg and Potgietersrust districts. There are not more than 500 in the Transvaal. (Fig. No. 11).

DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

pursuits. Consequently numbers are dwindling. The distribution remains much as in 1953, with herds in the Pietersburg, Soutpansberg, Letaba and Pilgrim's Rest districts. A small herd (too young to breed) has been taken to Loskopdam but it is not known whether they will become established. It is said that there are still some Sable in the New Belgium Block in the Waterberg district, but I have not seen them yet. The total number in the Transvaal does not exceed 800. (Fig. No. 12).

BLACK WILDEBEEST OR WHITE TAILED GNU

Connochaetes gnou

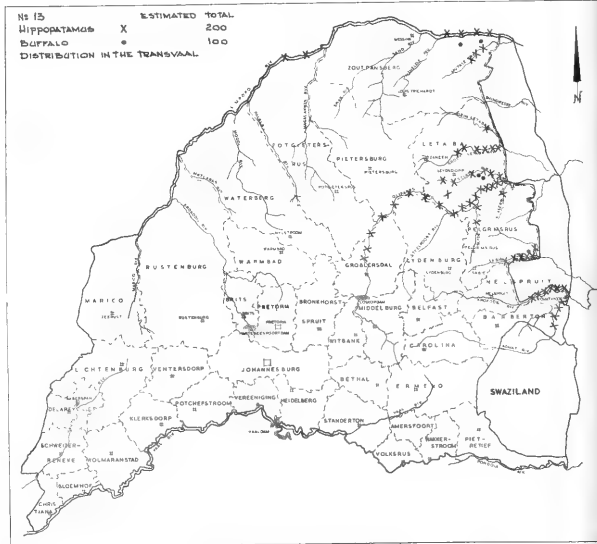
During 1945 there was only one herd of 46 on the farm Heuningkrans in the Wol-



maransstad district. In 1949 the late owner, Mr. Hoffman graciously donated twelve of these rare animals to the Transvaal Provincial Administration. These were taken to the S.A. Lombard Nature Reserve near Bloemhof.

Most of the present herds in the Transvaal originated from this herd, although some came from the Free State.

The number of black wildebeest in the Transvaal now number approximately 150. They are divided into 7 herds, and are well established. At least 40 excess bulls have been removed during the last 7 years to increase the breeding capacity. (Fig. No. 12).



DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

BUFFALO

Small herds occur in the eastern Soutpansberg, Letaba and Pilgrim's Rest districts. Occasional infiltrations occur along the boundary of the Kruger National Park. Buffalo disease in cattle, in the areas where Buffalo occur, makes their existence in the Transvaal precarious. The total number does not exceed 100. (Fig. No. 13).

Syncerus caffer caffer

HIPPOPOTAMUS

There are only a few Hippopotami in the western Limpopo. In the eastern Soutpansberg district they occur in the Limpopo, Mutali and Levubu Rivers. In the Letaba district they

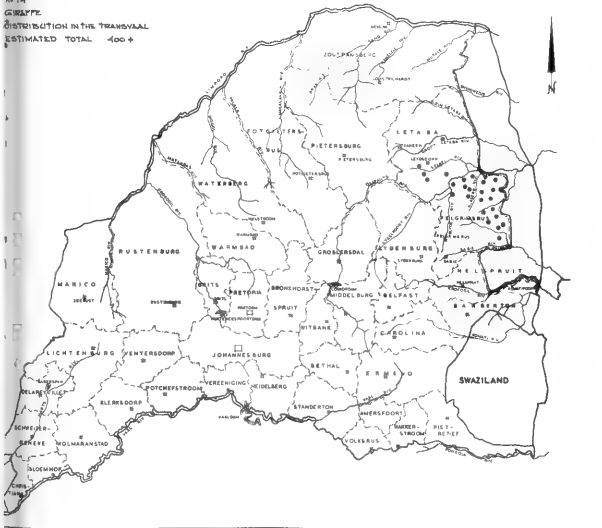
Hippopotamus amphibius capensis

No 14

GRAYE

DISTRIBUTION IN THE TRANSVAAL

ESTIMATED TOTAL 400+



are found in the Klein Letaba, Great Letaba, Selati and Olifants Rivers. In the Pilgrim's Rest district, in the Klaserie, Blyde, Sabie and the lower Sand Rivers. In the Barberton district they are in the Komati River. The northern boundary of the district is the Crocodile River, where they are also found, but this river which forms the boundary of the Kruger National Park is actually in the Park. In the Groblersdal and Lydenburg districts they are found in the Olifants River. An occasional Hippo goes up the Steelpoort River in the Lydenburg district.

It is most difficult to estimate their numbers; it can, however, be said that there are about 200 in the Transvaal. (Fig. No. 13).

GIRAFFE

Giraffe camelopardalis camelopardalis

At present this animal is found only in the Letaba and Pilgrim's Rest districts with the highest density in the latter. There seem to be a tendency lately for Giraffe to move southwards. A number of years ago they were very scarce in the southern parts and hardly ever crossed the Sand River. Lately they have become quite numerous between the Sand and the Sabi Rivers and have even moved as far as the Sabi River.

Because Giraffe sometimes break fences in cattle areas, they are becoming less popular with some owners. It is, however, encouraging to note that some of the biggest cattle ranches are protecting these animals.

There has been a decrease in their numbers since 1953. It is difficult to estimate their numbers as they move about quite a lot, but I would say that there are more than 400 in the Transvaal. A herd on the south bank of the Letaba was introduced into that area. (Fig. No. 14).

STEENBOK

Raphicerus campestris campestris

This species is most adaptable and thrives anywhere in the Transvaal from the cold highveld to the warm lowveld, except on the higher mountain ranges and close to inhabited centres. I do not know how many there are in the province; I do not even want to take a guess.

GREY DIUKER

Sylvicapra grimmia grimmia

This species is found practically everywhere in the Transvaal where the necessary bush cover exists and is at home on both the highveld and lowveld. Near populated centres these animals have become nocturnal and are holding their own like Kudu. No estimate of their numbers is possible.

BUSHBUCK

Tragelaphus scriptus

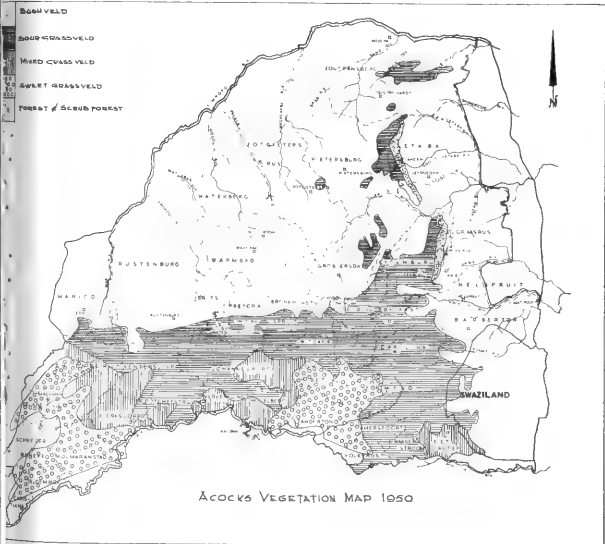
These buck are distributed north of the 26th latitude where the necessary dense riverine habitat exists, and in the Pongola area between Swaziland and the Natal border. In the subtropical belt and other areas where crops are cultivated under irrigation, they are slowly being exterminated on account of their nocturnal raiding habits. In areas where they do no damage, they can hold their own against heavy hunting pressure. Their numbers cannot be estimated.

I find Acock's vegetation map (1950) a valuable guide to the distribution of ungulates in the Transvaal.

The three dominant highveld species Springbok, Blesbok and Black Wildebeest were encountered on the sweet, mixed and sour grassveld. Of the three species I consider the Springbok the most selective. The densest population of Springbok occurs on the sweet grassveld which they prefer, although they also occur on the mixed and sour grassveld, but in smaller numbers.

DISTRIBUTION OF LARGER GAME MAMMALS IN TRANSVAAL

The Blesbok seems to thrive anywhere and has the densest population on sour grassveld. Where artificially introduced into the bushveld and even lowveld areas Blesbok seem to adapt themselves without any difficulty. The early introduction (1933) in the northern area was done by Mr. Percy Fyfe on the farm Lunsclip (Percy Fyfe Nature Reserve). These Blesbok were brought from the Free State and were introduced to the only little spot of sour grassveld in the surrounding bushveld (exactly the type of country they prefer). This is a known heartwater area, but the Blesbok survived and are still doing well. More than 1,000 Blesbok have been distributed from this Reserve into the northern bushveld and lowveld area where they are again doing well.



The distribution of Kudu coincides with Acock's Bushveld; even in the northern parts where patches of sour grassveld occur, Kudu are non-existent. This also applies to Impala, Blue Wildebeest and Zebra, but most of the last two species have already been cleared from their natural stamping grounds and in their present distribution do not demonstrate this fact as clearly as the Kudu does.

The present distribution of the Oribi coincides with Acock's grassveld, although it is known that they did occur in the southern lowveld.

The original distribution patterns were related to habitat requirements, but present distribution depends on the animal's ability to survive, and its economic and aesthetic values.

It is clear that the Eland, Roan and Hartebeest are slowly disappearing because they are easy to hunt and the meat is palatable. They are considered stupid buck by hunters. Next on the list will be the Zebra and Wildebeest. They compete with cattle as far as their feeding habits are concerned and they are also carriers of certain contagious cattle diseases. The Zebra has very little economic value at present.

The Impala has great economic value but it is not easy to keep them within ordinary fences and they can, therefore, not be properly protected. The Kudu, on account of its mobility and camouflage, can hold its own against heavy hunting pressure. The Blesbok and Springbok can easily be kept within ordinary fences and therefore enjoy protection. They also have high economic value. Nocturnal animals, like Bushbuck, Steenbok and to a certain extent Duiker, can survive under heavy pressure. The Oribi has become an animal of aesthetic value and is more or less protected by everyone. Although it is easy to hunt and has palatable meat, it still survives.

Where new areas are opened for agriculture the distribution of ungulate mammals will follow a definite pattern. The original distribution will shrink up to a certain point and then a new pattern will develop with artificial restocking, the extent of which will depend upon availability, adaptability and economic value of the animal. Blesbok and Eland have so far proved that they are adaptable. Because they are of economic value and are easily caught and transported, their new distribution pattern will cover the whole of the Transvaal.

The distribution pattern of most "game" ungulates will therefore undergo a continuous change in the development of the country.

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DISCUSSION

Mr. Attwell: The possible influence of fences in disturbing the natural movements of ungulates and thus intensifying or creating new spheres of interspecific competition has been mentioned earlier. Farming and fencing also introduce competition between the indigenous fauna and domestic animals. North of the Limpopo, there is a considerable body of opinion which opposes the introduction of domestic animals into marginal lands, but favours instead the "farming" and intermittent cropping of the indigenous ungulates already occupying these areas. Is it possible that the Provincial Administrations in South Africa might encourage a similar policy here, more especially in respect of poor farming land overstocked with domestic animals?

Mr. Kettlitz: I would very much like to support this suggestion but there are certain practical difficulties. In the Transvaal for instance, there are no vacant State lands, apart from the Bantu Reserves, and I do not think that either the Province or the State will be able to persuade private landowners to clear domestic stock from their properties.

Possibly the best method of achieving the desired result is to educate farmers to the potential economic value of game. In this connection, I wish to suggest that we should not too hastily condemn the introduction of game animals into areas where they are not known to have existed before. With the exception of the Oribi, I know of no game animal which is protected by farmers purely for its aesthetic value. But the more plastic and adaptable animals can be profitably farmed in many areas, an example being the Blesbok. With forms like the Kudu, however, which no fence will hold, the situation is more difficult.

- Mr. Grindley:* It has been shown in Tanganyika and elsewhere that a greater weight of meat per unit area can be produced when indigenous ungulates, rather than domestic stock are farmed. Could this not be used as an argument in the education of the farming community?
- Dr. Winterbottom:* Many farmers say that their endeavours to protect or farm game animals have involved them in losses because of widespread poaching.
- Dr. Omer-Cooper:* Others complain that the law is such that they are not allowed to sell the meat which they produce.
- Dr. Bigalke:* This is probably the first time that such a comprehensive set of information on South African ungulates has ever been brought together, and it has shown where our weak spots are. I suggest that this Society should ask the Provincial Administrations to give further attention to both the farming and conservation of these animals, especially rare forms. (A resolution to this effect was later adopted at the Annual General Meeting of the Society—Eds.).

C. J. SKEAD
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The use of early historical
references in the study of
bird and mammal distribution

Ethnographers have made good use of the earliest literature on the indigenous populations of the African sub-continent as a practical means towards an appreciation, not only of the life and times of those primitive peoples, but also of many a more remote problem touching even the archaeological field, such as the use of bored-stones, ostrich-eggshell beads and so on.

Although zoologists have dipped into and used these works from time to time there has been no real effort to extract data systematically volume by volume, and to present it in a readily available form with species related to localities and with the whole indexed for ready reference.

Having experienced the value of these early records in both mammal and bird work, not only for academic purposes, but also for their practical application in modern nature conservation, I feel that their value should be given some prominence.

The critical years are, perhaps, from 1652 to about 1800, although later works must be no more neglected than the more meagre records of the earliest Portuguese and French explorers before 1652. For most of us, translations of many books and papers will be necessary, but fortunately the careful records of the Cape kept under Jan van Riebeeck's orders and now translated into both English and Afrikaans, form a valuable starting point even though no zoologist was amongst his first colonists. It is here, for instance, that we read of South Africa's first efforts to protect game and to control vermin, and it is here, from history, that we are able to assess how the twin policy of fines for game poaching and bounties for vermin destruction have resulted in the steady extermination of the game and the stubborn persistence of much of the vermin!

My first serious introduction to the value of past journals came during a study of the spread of the Cattle Egret, *Bubulcus ibis*, throughout the sub-continent. With scientific literature meagre in its references, the obvious alternative was the historical literature, using the argument that, as the bird is so conspicuous, not only in its whiteness and in its flocking habits, but also in its preference for consorting with cattle and game, the traveller-diarist would surely make reference to it, the more so when it was considered that his mode of transport was the ox-waggon around whose oxen when outspanned the egrets would be likely to gather. But in no instance in the fifty or more appropriate books scrutinized did an author refer to this bird, whereas many a lesser bird, and its passing habits, received his

attention. On the basis of this negative evidence, plus the lack of later scientific and near-scientific records, it was safe to assume that the bird had not been a common inhabitant within recent times.

My next serious application to the historical record came when the National Parks Board of Trustees commissioned a documented list of the mammals which were known to have occurred in the Uitenhage and Cradock districts in order to help them plan the restocking of their national parks at Addo and Cradock (Skead 1958). For this I consulted at least 100 books of which about 30 provided reliable extracts. It proved a tough assignment involving, apart from the obvious theme, the thorny Bontebok-Blesbok controversy (in itself a major task of elucidation); and the controversial distributions of Burchell's Zebra *Equus burchelli*, the Blue Wildebeest *Gorgon taurinus*, the Gemsbok, *Oryx gazella*, the Black Rhinoceros, *Diceros bicornis* and many lesser mammals.

The work entailed in this project brought home to me the necessity for a series of extracted schedules ready for the use of zoologists. It was apparent, too, that, apart from any distributional data which would emerge, some appreciation of population dynamics beyond such oft-repeated inanities as "... game in countless thousands" would be obtained. More important, perhaps, was the occasional remark relating the mammal to its environment and the condition or nature of the vegetation, be it in drought or time of plenty.

But there were also the negative results. Why was there never a mention of Buffalo *Syncerus cafer* and Kudu *Strepsiceros strepsiceros* in the Great Fish River Valley north of Cookhouse, when they were frequently mentioned below that point? If we follow Sargent (1954) who has tried to correlate place names with mammal distribution, Buffalo would have been near Cradock, for was not Olive Schreiner's farm named "Buffelshoek"? Yet nobody has thought to write about Buffalo there, in country where they certainly could have thrived.

Such minor controversies serve a useful purpose in bringing a sense of caution and proportion into one's enthusiasm and make one realise that each deduction must be based on its merits, and on its probability in the light of other records and of what we now know. On this score it is most important that the extractor of historical records be not impressed or influenced by the repetition of a statement by author after author, if that statement is no more than an opinion, as in the case of the cock's-nest in a Penduline Tit's nest or the hermaphroditism of the Hyena. Such misconceptions are sometimes found in the distributional record too and must be guarded against, lest their repetition from author to author give them false provenance.

On the other hand, it not infrequently happens that, where an author's description has the reader confused as between one animal and another, some slight remark, even in a literary aside, touches on the very characteristic which marks that animal from its near relative, such as the white hairs on a Grysbok *Raphicerus melanotis*, absent in the Steenbok *R. campestris*. Another check on hasty assumption is the fact that the finding of a skull or bones in an improbable area (based on past records) may be explained by their having been taken there as a trophy, later to be discarded when the interest of the hunter evaporated. This is especially the case with elephant tusks, but even here other discoveries in contiguous localities can be used as corroborative evidence in association with an appreciation of the general environment.

Many of the early writers gave incomplete descriptions of the pigs they saw and it is largely because of this inadequacy that our knowledge of the distribution of the Warthog *Phacochoerus aethiopicus* is so lamentably inexact. Hyenas also suffer in this way, being too often lumped as 'wolves'. But in their case a lack of proper reference is of less concern than with the pigs because enough other data exist to present the picture as a whole. A strange lack of perception in the beholders occurs in their occasional inability to differentiate be-

tween the extinct Quagga *Equus quagga* and the Mountain Zebra *Equus zebra*, whose more complete locality-records we would dearly like to have.

Archaic nomenclature, tiresome though it is, need not present serious difficulties to the modern scientist when collating. Synonymies can help, particularly nowadays when teams of systematists, such as the South African Ornithological Society's List Committee, are rationalizing the nomenclature in the light of modern knowledge. But there is no doubt that in some cases the use of the same generic or specific name for different animals can be very trying. This is the result of an author's incomplete knowledge of his subject. Priorities were of little or no concern to him at that stage of African systematics, as instance Thunberg's, Lichtenstein's and Sparrman's errors in the use of the words *scripta* and *pygargus* in the then nomenclature of the Bontebok *Damaliscus dorcas dorcas*, the Springbok *Antidorcas marsupialis* and the so-called Harnessed Bushbuck *Tragelaphus scriptus*. At times, even colloquial names divert the thoughts, as when reference to the Mountain Antelope leads the reader to believe he is concerned with the Mountain Reedbuck, or Rooiribbok *Redunca fulvorufula*, only to find that the author means the Springbok. Here again some verbal aside, such as reference to the white dorsal mirror, suddenly clarifies the issue.

With experience one comes to assess the reliability of an author's perspicacity in the field and, may it be said, his veracity; yet, with one exception, none can be disregarded uncontaminately. The exception is Damberger (1801) of whose book Mendelssohn in his African Biography says: "...one of the cleverest volumes of fabricated travel ever produced."

The celebrated Thunberg, perhaps of more interest to botanists, is always worth reading if allowance is made for a certain credulousness to which he was prone. Le Vaillant enjoys considerable prestige amongst South Africans, yet is regarded with scant respect by his own country's scientists who prefer the greater reliability of Verreaux.

Even modern compilers and interpreters of the early journals, when converting old books and manuscripts into more readily readable form, liberally braced with explanatory footnotes and glossaries, often err in their deductions as in the instance where the extinct Blaauwbok, *Hippotragus leucophaea* is credited to the Transkei in error for the Bloubok, or Blue Duiker *Philantomba monticola*.

In the matter of readability and accessibility of the old records the very greatest credit is due to the Van Riebeeck Society, not only for being the means whereby these records are preserved by their very dissemination throughout the country, but also in the high standards demanded of and produced by their author-collaborators. Zoologists cannot be too grateful to the Society for this service.

Whereas the early records, for obvious reasons, tend to emphasize the larger mammals and larger birds, and even the most conspicuous of these, the smaller creatures are not neglected by the more competent authors. It is here that a well compiled and indexed catalogue is of the greatest value because the amount of work involved in searching for the few records in volume after volume (never properly indexed), might well deter even the most enthusiastic, whereas with each record extracted once and documented in the correct place, all this is saved.

With a background of these facts I initiated a system for use in the Kaffrarian Museum whereby, as each volume was read, be it Burchell, Barrow, Thunberg, Livingstone, La Trobe or many another, the relative mammal record was noted down under the following headings across a sheet of foolscap:

DATE	PAGE	LOCALITY	MAMMALS SEEN
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Thus it became possible to know at the flick of a page where and when Burchell had met, say Blesboks, or any other likely mammal. If the enquirer needed more detailed information, the page reference showed him where to find it in the original printed work. The great

importance of this catalogue became evident when it had built up over many authors and their volumes. The general picture of a mammal's distribution then came into perspective and, if necessary, could be plotted onto distribution maps. As a side issue, the cataloguing of the routes taken by the travellers became of historical as well as of zoological value and, to date, 31 such volumes have been condensed into a single filing cover, each mammal indexed for ready reference, but with the localities still solely in need of their own index.

Since joining the staff of the Percy Fitzpatrick Institute of African Ornithology and therefore having to concentrate on bird-life, I have started a catalogue which differs from the mammal catalogue in that it does not act also as a chronological record of a traveller's day to day journey. Each extraction is still in chronological order but only the actual bird records and their localities are noted. The page headings in this instance are:

REF. NO.	PAGE NO.	YEAR	LOCALITY	BIRD DATA
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Books listed in the bibliography are numbered as the extractions are made, e.g. No. 6 may be Barrow and No. 8 Lichtenstein; this is for convenience of compilation. The number, 6 or 8, appears under the heading Ref. No. and the page on which the bird reference is found appears in the next column. The other headings speak for themselves. The benefit of this system over that for the mammals is that under Bird Data far more information is extracted and entered where this is deemed necessary. But, as with all books, the essential ingredient in this idea is an adequate index. To that end the index is compiled as the work proceeds. After an hour or two of extracting and entering, the index is written up, the task of only a few minutes, but one which if left until a bulky tome is erected becomes arduous and formidable.

In the course of the next few years with my work taking me to many out-of-the-way places and into homes where family treasures lie hidden, it is hoped to unearth journals and manuscripts which may reveal fresh facts on our fauna. I firmly believe that such works exist and, although most will be more historical than zoological in their content and value, they will be well worth looking for.

Nobody need be deterred from using the old records merely because they are old and because they were written by people whose knowledge of the country and its animals was inadequate, as indeed it could hardly have been otherwise. Provided the safeguards and checks I have suggested are employed, a fair appraisal of events is always possible, and always valuable.

SUMMARY

This paper is a brief appreciation of the value to be obtained from studying the journals, etc. of early settlers and travellers in the compilation of distribution records and charts. It emphasizes the difficulties of interpretation and suggests precautions, and hints at pitfalls when extracting data. Finally, an outline of a system for recording extracted mammal and bird distribution notes to the best advantage is presented, emphasis being laid on the necessity for a good index in each case.

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DISCUSSION

Mr. Liversidge: Has Mr. Skead explored the diaries of Ludwig Krebs who collected extensively in the 1820's and sent his material to the Berlin Museum, most of it labelled simply "Inner Kaffraria"?

Mr. Skead: I know of the diaries but have not investigated them.

Mr. Davis: I have also come up against the problem of Krebs type localities which sometimes appear to be wrong. There is for instance, a *Steatomys* recorded from Graaff Reinet which simply does not occur there.

Dr. Winterbottom: Did Andrew Smith ever produce a diary of his journey to Namaqualand? Many new forms which he described from that area have no detailed locality.

Mr. Skead: I do not know whether there was such a diary, but the trouble about Namaqualand is that named places were so few and far between.

Dr. McLachlan: I have also thought it possible that there might be a diary of Andrew Smith, recording the Namaqualand journey; but Professor Kirby says there was none.

Dr. Pringle: Unpublished records may also form important sources of information. For instance Wahlberg's diaries (ca. 1840) are in the archives of the Uppsala Museum but have not been published.

R. LIVERSIDGE

PORT ELIZABETH MUSEUM.

Distribution of birds
in relation to
vegetation

INTRODUCTION

To say that in the preparation of this paper my mind has swung back and forth in considering the possible importance of vegetation for birds, is simply to express the delightful unpredictability of bird distribution. For two points stand out from the many analyses made: The first is that a species in southern Africa so often changes its habitat from one end of its distribution to the other, that it is not necessarily safe to assume that because it is a forest bird in the south it will be a forest bird in the north. The second is that abnormal conditions such as coldness in the tropics or wetness in the south-west arid regions produce peculiarities that cloud the normal pattern of distribution.

This study of bird distribution concerns the species, not families or orders, as suggested by Winterbottom (1960) for the determination of faunal affinities. The approach here adopted is that of Chapin (1932) who states: "Each species must be studied by itself, after which it may often be included in some general scheme that will enable us to view in a *not too unnatural perspective* the wider aspects of bird distribution" [my italics]. In the attempt at such an analysis, the distributions of the first 600 species numbered in Roberts (McLachlan & Liversidge 1957) have been plotted. Time prevented the entire 875 being included. It is inevitable in such a vast project to lose some detail of the finer distribution lines or extremities of distribution in the endeavour to reduce the pattern to coincide with the accompanying six maps (Figure 1). The species chosen out of the first 600 are those which have been illustrated by maps in McLachlan & Liversidge; the sea birds and those that are not common or sufficiently wide-spread have been omitted, leaving a total of 423. These 423 include non-breeding migrants many of which have distribution pattern similar to locally breeding species, though naturally these birds would not be included in faunal groupings for zoogeographic consideration.

BIRD DISTRIBUTION PATTERNS

The patterns have been separated into east, north-east, north, central-north, west/north-west and south components for convenience and because this seemed to be the only obvious grouping. Not covered in these maps are a total of 61 species found throughout southern Africa and 45 species which have an unusual distribution, but these are listed in Table 1.

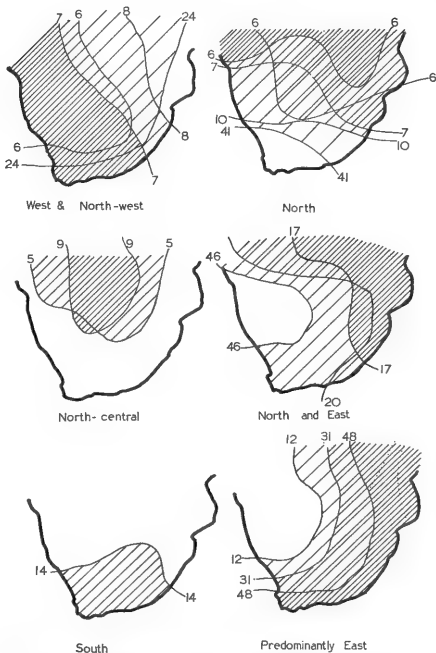


Fig. 1. Illustrating the generalised distribution patterns of South African birds. Each map has marked the number of species that occur on the line of limit of each pattern.

DISTRIBUTION OF BIRDS IN RELATION TO VEGETATION

TABLE 1

Area	No. of Birds	Percentage of No. Mapped of 423	Percentage of Total considered 600
Uncommon or very restricted	177	—	30
Whole Union ..	61	14	10
Specialized and restricted	45	11	7½
Predominantly east ..	91	21	15
North and east ..	83	20	14
North-central ..	14	3	2
North	70	17	11
West/north-west ..	45	11	7½
South	14	3	2
Total	423	100	99

The group of 45 species with distinctive patterns could perhaps be reduced in number with more detailed knowledge and unfortunately it is from this group that many false impressions are gained. It can be seen that the east and north-east components have between them 41% of species and thus more than any other section. Many species unmapped would probably fall into this group since they include the southern extension (down the east coast) of many so-called tropical species. Thus the most important and varied group of bird species are those of south-east Africa; they are numerically greater than those found in the south-west (arid) regions.

The many finer points which unfortunately have been omitted in the generalized maps are more important from the vegetational point of view. Thus we find many limits of bird distribution which fit the finer vegetation types mentioned below. This does not only apply to our own regions as the following quotation from Hall (1960), who refers to Angola, indicates: "Repeatedly it will be found that birds of many different families have similar specific or subspecific ranges which lie along the same boundaries and co-incide with the limits of one or another type of vegetation". Some of the commoner minor limits of distribution are mentioned and illustrated later.

VEGETATIONAL DISTRIBUTION

In birds there are only two sources of mapped distributions in Southern Africa (McLachlan & Liversidge 1957, Skead 1960) apart from detailed taxonomic papers on individual species. Plants however, have received a variety of cartographical representations

ranging from the generalized C.C.T.A. map (Keay 1959), suggested for this conference, to the very detailed veld-types published by Acocks (1953). Two South African botanists whose work appears largely to have been overlooked and yet whose maps are most useful from the ornithologist's point of view are Adamson (1938) and Pole-Evans (1936). For example both show a tongue of a vegetation-type north from Kuruman which co-incides with the limits of distribution of several lark races. In the confusion of the detail of Acocks (1953) this region is not apparent. There seems to be some disagreement on whether the Kalahari thornveld should be included in southern savanna or not. From our point of view it is rather a large important tract of land. If "life-form" has any importance in vegetation types, then it would seem right to include the Kalahari in the savanna as most South African botanists have done. "Life-form" refers to the general appearance, size, foliage, etc., that a plant assumes under local ecological conditions. The author prefers the use of Pole-Evans map for the ecological aspects of animal distribution but Keay's map has been used as the recommended map for this conference.

FACTORS INFLUENCING DISTRIBUTION OF VEGETATION

Adamson (1938) considers that the broader vegetational zones such as forest and savanna are influenced by climate. The lesser vegetation-types are influenced by climatic, physiographic, edaphic, biotic and historical factors. On the smaller divisions there is argument whether climatic or edaphic factors are dominant in their influence over the vegetation. It would appear at least in the eastern Cape that edaphic factors are more important as the following example shows. The typically "Cape" vegetation extends east to Port Elizabeth; there are, however, patches in the Alexandria division and in the Port St. John division which grow on outcrops of the "Cape" geological system in these two areas, though the climate and the surrounding vegetation is of a more subtropical nature and certainly not a winter rainfall area.

Of the climatic factors the rainfall is the most important. This can be seen from the general similarity between the patterns of the mean average rainfall map and the vegetation map. The temperature appears to have a completely independent pattern, associated with altitude but, except along the low-lying east coast, showing no clear agreement over the rest of the country. Frost patterns agree roughly with the isotherms.

COMPARISON OF PLANT AND BIRD DISTRIBUTIONS

Using the broad zones of the C.C.T.A. map, there are 11 species of birds which have a distribution similar to that of the southern savanna and nine which conform to the same veld-type if the Kalahari thornveld is included (Table 2). Two species conform roughly to the south-west arid region, viz. Stark's Lark *Spizocorys starki* and Red-eyed Bulbul *Pycnonotus nigricans*. Three species agree with the south-west Cape, namely Victorin's Scrub-Warbler *Bradypterus victorini*, Orange-breasted Sunbird *Anthobaphes violacea* and the Cape Sugarbird *Promerops cafer*.

There appears to be little correlation between bird distributions at the species level and vegetation types. However, as already mentioned the boundaries of the two very often co-incide along part of their limits of occurrence. The difficulty appears to be largely due to the variability of birds' habits. As Winterbottom (1959) states with regard to certain species "although characteristically or exclusively forest birds in the south, further north they become birds of the savanna woodlands and are often absent from true forests". This argument may be applied in reverse and not confined to forest and savanna alone. It is not surprising therefore that the birds do not fit in with single vegetation-types. Despite this discrepancy in detail we need look no further than the same article by Winterbottom to

TABLE 2
BIRDS OF THE SAVANNA

Excluding Kalahari-thornveld

White-faced Duck	<i>Dendrocygna viduata</i>	(100)
Brown snake-eagle	<i>Circus cinereus</i>	(145)
Little Sparrowhawk	<i>Accipiter minullus</i>	(158)
Crowned Crane	<i>Balearica regulorum</i>	(214)
Emerald-spotted Dove	<i>Turtur chalcospilos</i>	(321)
Green Pigeon	<i>Treron calva</i>	(323)
Black Cuckoo	<i>Cuculus cafer</i>	(344)
Great Spotted Cuckoo	<i>Clamator glandarius</i>	(346)
Lesser Honeyguide	<i>Indicator minor</i>	(442)
Golden Oriole	<i>Oriolus oriolus</i>	(519)
White-browed Scrub Robin	<i>Erythropgia leucophrys</i>	(588)

Including Kalahari-thornveld

White bellied Stork	<i>Sphenorhynchus abdimii</i>	(78)
Pallid Harrier	<i>Circus macrourus</i>	(168)
Montagu's Harrier	<i>Circus pygargus</i>	(170)
Harlequin Quail	<i>Coturnix delegorguei</i>	(190)
Lesser Gallinule	<i>Porphyrio alleni</i>	(209)
Wattled Crane	<i>Bucconas carunculatus</i>	(215)
Bronze-winged Courser	<i>Rhinoptilus chalcopterus</i>	(280)
Cuckoo	<i>Cuculus canorus</i>	(340)
Scops Owl	<i>Otus scops</i>	(363)

realize that his three avifaunal divisions are in actual fact coincident with vegetational divisions, called by him "winter-rainfall area, temperate forest and karroo". The winter rainfall area is typically Cape vegetation.

Chapin (1932) says bird dispersal in the Congo is determined by climate which acts upon birds through the vegetation "save perhaps the cold of the mountains". In an earlier paper (Liversidge 1959) I came to the conclusion that temperature was the principal restricting factor for species of tropical montane forests. It is evident now on further analysis that this is due to the extreme conditions within the tropics since, in the southern ranges of these montane species, temperature appears to play no part and they occur on the much hotter Karoo plains. Winterbottom (1959) also noted a change in habitat of Karoo species which extend into the winter-rainfall area. Hall (1960) remarks upon the same thing in Angola with regards to birds of the plains when they occur in the mountains. Not only is there a variation of habitat, often at the limit of a bird's distribution, but there is often a change of status from resident and local over most of the range to being a bird of definite migratory behaviour.

Individual plant species or types are often associated with a bird's distribution. The palms for example of the genera *Elais* and *Rhaphia* are associated with the major portion of the distribution of the Palm-nut or Egyptian vulture *Gypohierax angolensis*. The Palm swift *Cypsiurus parvus* occurs where it can nest and roost amongst palms though it is interesting to note it has recently taken to breeding upon bridges. However, here again there are multiple factors involved. In Rhodesia for example the Streaky-headed Seed-eater *Poliospiza gularis* occurs strictly in *Brachystegia* woodlands (Liversidge 1959) but in the eastern

Cape no such woodland exists and the same bird occurs in totally different scrub vegetation. Another species which is associated with a particular plant, namely the Sword Plant *Sansevieria*, is the Spectacled Weaver *Hyphantornis vociferus* which uses fibres stripped from the leaves for its nest. This association is quite marked in the eastern Cape where the weaver nests in the veld away from water. To the north the Spectacled Weaver is associated with water and this factor is probably responsible for its absence in northern Bechuanaland where a belt of *Sansevieria* occurs from Maun towards the east.

Associations between plant and bird species are evidently long established since morphological adaptation has occurred in some species. Irwin (1959) shows that what was considered to be a single species, the Black Tit *Parus niger* actually has two forms, one of which occurs on the western part of the range and is associated with *Acacia* woodland; and the other, a heavier billed bird, occurs in *Brachystegia* woodland. Where islands of one type of vegetation are found within the other, populations of the expected form of Black Tit are always present.

DISCUSSION

From the evidence here adduced, bird distribution seems to be closely associated with vegetation but the vegetation-types, as such, show little agreement with bird distribution patterns. It is therefore unlikely that vegetation, considered from a botanical point of view, is in itself of major importance. "Life-form" is probably of some importance. For example, some predators obviously require perches which give a suitable vantage point in order to spot their quarry. Further many birds are dependent upon flowers or fruits as a source of food. For example, various sunbirds (Nectariniidae) are attracted to different vegetation types depending upon the flowering of suitable plants. The full details are uncharted, but in June and July aloes flower at Addo; in August and September, the kaffirboom *Erythrina caffra* flowers at Alexandria; and in January and February *Brunsvigia* flowers along the coastal dune. Sunbird populations which are noticeably larger than normal occur in these areas at the times given. Aloes, however, may flower in different parts of their range at different times, as much as four months apart over a distance of 150 miles (as from Port Elizabeth to Amatola Mountains). Yet it seems more likely, though we have no facts as yet, that individual sunbirds do not follow the successive flowering of a given plant in adjacent districts but remain in the same broad area and change their food plants. The Knysna Lourie *Turacus corythaix* remains, on the whole, localized but shows definite seasonal movements within its habitat according to the ripening of the various species of fruit it eats.

Thus while vegetation may influence the distribution of some species locally, it is not the main factor with which we may associate bird distribution. There must be some factor influencing both. A brief inspection of the climatic factors indicates that the rainfall patterns agree most closely with bird and plant distribution patterns. This is in agreement with Chapin. However, Poynton (1961) shows the "Tropical" east coast element is possibly associated with a minimum temperature range. This can only be true of the warmer areas since mean absolute minimum temperature patterns show no correlation with bird patterns except for the warmer isotherms. This presents the possibility that geographically the factors influencing bird distribution vary; thus within dry areas, rainfall is important; in warmer areas isotherms are important. Dominant climatic factors in a region influence the birds of that area and where these dominant climatic factors vary, from region to region, the main factors influencing bird distribution of these regions also vary.

If this variability of factors influencing bird distribution is accepted then it is easy to understand how the different concepts in avian distribution fail.

Ornithologists tackle the problem of geographical distribution in three ways. Firstly there are the so called "life-zones", zoogeographical regions based primarily upon isotherms.



Fig. 2. The biotic provinces of Southern Africa as suggested by McLachlan and Liversidge.

These life-zones have become the classical units of broader zoogeography and the original zones, such as the Ethiopian Region proposed by Sclater, are generally accepted today. The second concept is that of *biomes*, mainly supported by the American ecologists and formulated upon natural areas based upon so called climax vegetation. Unfortunately from the mapping point of view, *biomes* do not form continuous areas. This gave rise to the third concept, the so-called *biotic provinces*, which in fact amount to an attempt to couple *biomes* to geographical distributions by making continuous uniform units. Biotic provinces while not being highly satisfactory are in general use throughout the world.

The biotic provinces for southern Africa have been published (McLachlan & Liversidge 1957, and Winterbottom 1960) (Fig. 2). In practice distribution of birds does not fit satisfactorily into biotic provinces, though many species share boundaries similar to those illustrated. The names and areas applied to the biotic provinces, however, are in common use.

These biotic provinces cut across major climatic regions. The subdivisions proposed by Winterbottom (1960) for the western Cape are in agreement with these findings. For the Transvaal highveld and lowveld, it would seem more satisfactory to revert to the "forest" fauna and "steppe" fauna divisions suggested by Reichenow rather than western and eastern designation as commonly used (Chapin 1932).

Before any conclusions can be drawn about the bird faunal units of the area between the Zambezi and Vaal systems it is obvious that a much more detailed knowledge of the dispersal of birds up to the south equatorial divide is needed. In fact a picture of the whole Ethiopian region seems essential and with the checklists and books recently published it should be possible to make such an analysis.

SUMMARY

Analysis is made of distribution patterns of 423 species which fall into the divisions east, north-east, central, west-north-west and south. Vegetation maps and factors influencing vegetational distributions are discussed. Plant and bird distribution is compared; there is only a poor correlation of broad zones, but a close matching of boundaries with vegetation types in many cases. Individual species are influenced by certain types or species of plants. It is concluded that dominant climatic factors influence bird distribution and where such factors change the dominant factors influencing bird distribution also change. The concepts of life-zones, biomes and biotic provinces are discussed.

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DISCUSSION

Prof. van Zinderen Bakker: In these discussions there has been a tendency to consider the influence of single factors separately, but this procedure may mislead. We are dealing with living organisms for whom such matters as climate, soil, vegetation and temperature form an interacting complex.

Mr. Liversidge: I agree, and think that Dr. Poynton, for instance, gave too much emphasis to the effects of temperature. However, I felt that vegetation represented one end-point of the "interacting complex", and thus expected to find some coincidence with avian distribution, but did not.

Prof. van Zinderen Bakker: Temperature is probably the primary factor, influencing all others when it changes.

Dr. Poynton: I certainly do not regard temperature as the only factor determining distribution and agree with Mr. Liversidge that rainfall is limiting in the west. However, in regions where rainfall is not limiting and where ecological conditions are generally constant, temperature effects distribution. It acts directly and not indirectly as does precipitation. In this, it is important to consider the distribution of major systematic groups rather than of individual species.

Prof. Ewer: I am disturbed by this "lumping" tendency. The things which will effect distribution, especially amongst birds which are free of so many limitations, must be closely related to the individual species' way of life. Black-headed Gulls in England, for example, have become inland birds, changing their distribution completely, following a change in habits. It seems a doubtfully valid procedure to throw all species in a group together and expect a meaningful result to emerge; and I become increasingly sceptical regarding the significance of attempts to reconstruct a phylogenetic zoogeographical picture. We are forgetting how competition may affect distribution and that speciation may be in active progress. We are dealing not with static things, such as so many cities or mountains, but with living organisms.

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A note on zoogeographical
limits in South-East Africa,
as suggested by the avifauna

In a previous paper (Winterbottom, 1962), I suggested that the whole area of the East African littoral from Kenya to Knysna forms a single zoogeographical District, divisible into two or more sub-districts; and that the northern boundary of the southern sub-district lay in Zululand. In my map, I accepted the line drawn by McLachlan and Liversidge (1957), at about Sordwana Bay. Since my paper was written, there has been a Symposium on geographical distribution in Zululand (see, especially, Poynton, 1960, 1961) and the evidence from other groups of animals, as well as from plants, strongly suggests that the major faunal and floral change occurs further south, at St. Lucia; and that it is a much more substantial change than I had concluded from studying the birds. It therefore seemed worth while to re-examine the ornithological evidence with this opinion in mind.

In my previous paper, I reported that I had drawn up a list of 194 characteristic birds of northern Mozambique. "Of this list, 147 species (79 per cent) reach Zululand and 100 (52 per cent) Pondoland." This does not, in itself, suggest that the change taking place in Zululand is a major one, since 37 species drop out between northern Mozambique and Zululand and 47 between there and Pondoland; though the rate of loss is certainly very considerably accelerated (roughly one every three miles between the Tugela and the Umtamvuna as against one every twenty miles between the Zambezi and the Usutu and one every sixteen miles between the Usutu and the Tugela).

Analysis of the southern limits of range of the 47 species which do not reach Pondoland gives the following results:

Four (*Cossypha heuglini*, *Corythaixoides concolor*, *Tchagra australis* and *Eremopteryx leucotis*) do not reach as far south in Zululand as St. Lucia.

Seven (*Batis fratrum*, *Nicator gularis*, *Eurystomus glaucurus*, *Mirafraga rufocinnamomea*, *Bradornis pallidus*, *Nectarinia bifasciata* and *Eremomela icteropygialis*) stop at St. Lucia.

The remaining 36 species reach at least to the Tugela River and many of them further still.

Of the seven species which stop at St. Lucia, *Eremomela icteropygialis* reaches much further south (to the Olifants River) in the west.

There are four species (*Nectarinia neergardi*, *Apalis ruddi*, *Hypargos margaritatus* and *Serinus citriniceps*) whose range is confined to the area between Inhambane and St. Lucia and only the last-named of these does not reach St. Lucia. Thus the total number of species for which St. Lucia is the southern limit is nine, or ten if we count the *Eremomela*.

In my original assessment, I did not consider the water-birds. Of these, there are 20 species which occur south of the Tropic only in the coastal strip from Zululand to the Eastern Cape or even further south-west. Of them, only five (*Anastomus lamelligerus*, *Ephippiorhynchus senegalensis*, *Vanellus crassirostris*, *Sterna bengalensis* and *Ploceus xanthopterus*) reach their southern limit in Zululand; and only one of these, *Vanellus crassirostris*, has its limit at St. Lucia. *Anastomus lamelligerus* may, perhaps, be added, though it is not a regular inhabitant south of Ndumu.

While, therefore, a shift of the boundary between what I have called the East African Coastal and the Tropical Corridor* sub-districts from Sordwana to St. Lucia can be supported on ornithological grounds and is obviously convenient to bring avifaunal divisions into correspondence with those based on other groups, bird distribution lends little support to the view that a major faunal change occurs at this point.

Poynton (1960) has shown that the distribution of Amphibia appears to be closely controlled by temperature and rainfall and not by vegetation (though this argument in respect of the south-west Cape seems to me insecurely based); and that there are two major constituents of the South African fauna, one tropical and the other centering on the south-west Cape. These concepts, unfortunately, do not fit bird distribution at all, despite Poynton's special pleading (1961). The major components of our bird fauna would seem to be a western, desert element, a northern savanna element, and a north-eastern forest and scrub element. There is also a montane-temperate element, whose relationship is difficult to assess but which would appear to be the result of an invasion from the north with some subsequent speciation in the south and south-west. This conforms to Levyn's view (1952) of the origin and affinities of the Cape flora, though amongst birds, evolution in the south has been very much less marked than in plants, or, apparently, than in Amphibia.

In this connection, however, we may note Acocck's view (1953) that the non-succulent part of the karoo flora has been derived from that of the south-west sclerophyll. This might imply that the western, desert avifauna of southern Africa has evolved from that of the sclerophyll, with which it has still obvious affinities; that the much greater differentiation in sclerophyll plants, as contrasted with birds, is related to the small geographical area of the sclerophyll and the relatively immensely greater mobility of birds; and that the severe conditions of the desert have prevented a rich Amphibian fauna from differentiating there, as it has in the sclerophyll. This last is an example of the differences likely to arise in severe environments between homoiothermal and poecilotheimal animals.

If this interpretation be correct, then the equivalent of Poynton's Temperate fauna in birds is the whole South-West Arid District, as I have defined it, much of which falls into one or other sub-division of Poynton's Transitional Zone (chiefly his Western Temperate Transitional and the "subtraction transitional" area between that and his Western Tropical Transitional) when the Amphibia are taken as the basis.

It is interesting to compare this situation with that of the Winter Rainfall area in Australia, and particularly in Western Australia. A study of Gentili's paper (1949) makes it clear that the sub-humid, and even the semi-arid, areas of western and south Australia are divided by an arid belt which reaches the coast of the Great Australian Bight and isolates the two areas (his Maps 5, 6, 7 and 11), though this isolation is now somewhat less than in the early Recent. No such isolation occurs in South Africa, where sub-humid climates and vegetation patterns link the humid and forested areas to the west and east, though it is possible that in the last arid period, such isolation did exist in the Port Elizabeth area, where the present annual precipitation effectiveness is 35 (the dividing line between sub-humid and semi-arid). Poynton has pertinently pointed out to me (*in litt.*) that the term "Tropical Corridor" is misleading, as it implies a connection between two other areas, whereas the area so designated by Gill and by me, is a progressively attenuated extension of the tropical area at one end and terminates abruptly at the other. Another name will have to be found.

arid being 32) and karoo types of vegetation approach to within 40 miles of the coast. Even this, however, would only isolate the sub-humid areas, whereas in Australia, the semi-arid areas are isolated likewise. Nevertheless, there are some indications of a dicentric pattern, similar to that shown by a number of Australian birds, in South Africa, as in *Promerops* (*caffer* in the west, *gurneyi* in the east) and *Chaetops* (*frenatus* in the west, *aurantius* in the east). But it would take us too far from the main subject of this paper to pursue the point further here.

SUMMARY

1. It is concluded that, in birds, the division between the northern and southern sections of the East Coast Faunal Province should be brought south to St. Lucia Bay.
2. In birds, however, this is not a major boundary.
3. It is suggested that the avian equivalent of the amphibian "temperate fauna" is that of the whole South-West Arid District.
4. The African south-west corner has never been as isolated as the Australian south-west; but some indications of isolation can be detected.

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DISCUSSION

- Dr. Stuckenberg*: With reference to Acock's view on the non-succulent part of the Karoo flora, it may be added that he believes that the succulent component was derived from the Fish River flora. However, I doubt whether the Cape flora and birds should be spoken of in the same breath as one is so very much older than the other. Regarding avifaunal boundaries on the east coast, there was a recent statement by Vincent that a large number of bird species have withdrawn from Natal (following agricultural expansion) into Zululand. There is historical evidence of a similar withdrawal of certain invertebrates. Finally, I would like to suggest that the importance of the Zambezi on the Moçambique plain is often underestimated. It certainly forms a natural boundary for invertebrates, not simply as a river, but probably because the north bank is not well-forested whereas the south bank is.
- Dr. Winterbottom*: The withdrawal of various animals from Natal into Zululand seems to support my view that this is not a major boundary.
- Dr. Theiler*: In considering distribution patterns it is easy to overlook the influence of differences on a vertical scale. The environment at soil level may be very different to the environment in the same place, a few feet above the ground. Amongst the ticks, which often have distribution patterns entirely independent of the distribution of their mammalian hosts, a boundary does exist at St. Lucia. Perhaps the differences of opinion between the students of amphibia and birds may simply be the result of dealing in different environments, one at soil level and the other above it.
- Dr. Meester*: For each animal there may be a different set of factors producing different areas of distribution. It would seem that we are not yet at a stage to lay down rules for groups, but must still concentrate on understanding individual species patterns, rather than attempt interpretation on a large scale.

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The significance of valleys
as avian zoogeographical
barriers

SYNOPSIS

Consideration is devoted mainly to major valleys lying wholly or largely in the Federation of Rhodesia and Nyasaland, of which one or other of the authors has extensive personal experience. But an account is also included of the significance of the Albertine and Kenya Rifts. No attempt is made to discuss the more northerly Rifts, knowledge of which is probably insufficiently documented.

From a study of avian distribution, it is demonstrated that the Limpopo and Zambesi Valleys, and the Luangwa, Nyasa/Shire, Albertine and Kenya Rifts are all significant barriers to dispersal of species, due to the sharply different ecological conditions in the hot low-lying bottoms, compared to the higher ground on either side. Instances of subspecific differences are also given.

The position may be summarised as follows:—

			<i>Number of species confined to—</i>		<i>number of subspecific differences on two sides*</i>
			<i>(a) South side</i>	<i>(b) North side</i>	
Limpopo	15	31	15
Zambesi	8	35	30
			<i>(a) West side</i>	<i>(b) East side</i>	
Luangwa	22	8	9
Nyasa/Shire	19	4	13

Various anomalies are mentioned, such as subspecific differences on the two sides of the Nyasa/Shire Rift, with in some cases the western, in others the eastern, form the same as in Southern Rhodesia.

* In the case of the Luangwa and Nyasa/Shire, several instances of closely allied, geographically replacing, species-pairs included.

Discussion of the Albertine Rift is confined mainly to passerine species inhabiting evergreen forest. Thirty-two lowland species do not extend east of the Rift. The fauna of the montane areas of Kungwe, Marungu and Ufipa is relatively poor. The Kenya Rift is also an important barrier, being both an obstacle to the passage of certain species and an isolating factor which has resulted in the subspeciation of a number of species occurring on both sides.

INTRODUCTION

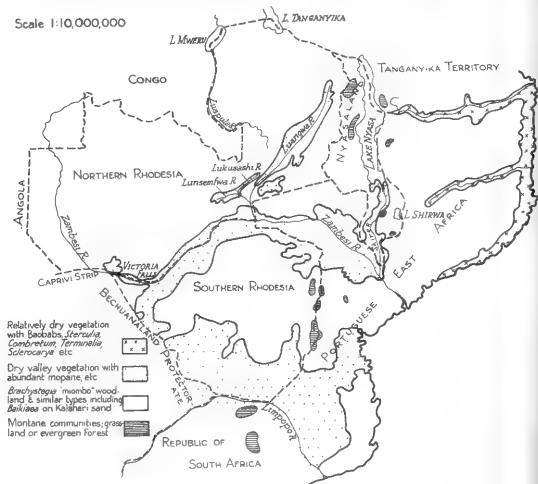
This paper focuses attention upon the faunistic significance of the Rift Valleys of Africa and some analogous gaps. Flint (1959), evidently referring to the Albertine and Kenya Rifts, writes that "Lower Pleistocene sediments locally postdate the main faulting: minor faulting has occurred even in very late Pleistocene times". Moreau (1952) has pointed out that the Pliocene was a period of much tectonic disturbance in Africa, but that only in the Pleistocene, and mainly in the last three quarters of a million years, did there develop the most marked rifting which gave rise to the levelling down in altitude of the floors of the present Lakes Nyasa, Tanganyika and Albert. The Kenya Rift took on its present form at the same period. In terms of geological time the Rift Valleys are thus recent formations, but as the review which follows indicates, their effect upon the distribution of birds is often pronounced, one inference being that the floors of these valleys are ecologically different from the country at higher levels on either side and, as such, provide an unfavourable biome to species living in the environments at higher levels. Thus the study of these valleys is of importance in the analysis of population systematics, since geographical isolates are often the apparent consequence of the rifts and similar valleys. It will be clear that there are enough geographical isolates in Africa of this type to allow for extensive speciation.

Apart from the fact that different subspecific isolates are to be found on either side of these valleys, it would appear that the valleys may have operated also as an absolute barrier to the dispersal of species. One obvious example of this appears to be provided by the Limpopo system, for a number of South Africa endemics have not crossed it to extend further north, whilst conversely tropical species extending south into Southern Rhodesia have not crossed it to extend still further south. Similar instances are given for the other examples discussed. The overall picture which emerges is that species characteristic of a particular biome are highly sensitive to ecological conditions provided by a different biome, and fail to cross it even though the actual gap is often only a few miles in width. This is of course wholly in keeping with the data set out by Moreau (1952) when he pointed out how birds tend to be strongly specific in Africa to certain main biotic types. Ornithologists have now demonstrated the truth of this in a number of ways; and evidence could be presented to show how speciation has occurred, or is apparently occurring, simply through populations of certain species having adopted different biomes, many instances of which are given by Benson *et al.* (1959). The field which still remains almost wholly untouched is to ascertain what factors associated with a given biome attach a particular bird species to it in a way which inhibits movement into or across another biome. In some of the most contrasting examples, as where montane forest species are separated by a dry area, one may suspect with good reason that certain very obvious problems of adjustment from high altitude, wet and shady montane forest to arid scrub will prove insurmountable obstacles, even though one cannot particularize about how such adjustments affect the organism. But in some of savanna instances this contrast must be considerably less severe, and it remains to explore just how the components of a biome do in fact interact with an organism to have such a profound inhibiting effect upon mobility.

Winterbottom (1959), in a general paper on the zoogeography of the South African avifauna, has discussed, necessarily only briefly, the significance of the Limpopo and Zambezi Valleys as barriers. His figures of species restricted by one or other of these valleys are all considerably higher than those given in the present paper. We have certainly been more

exacting in our inclusions. Thus Winterbottom gives 67 species as present in the Transvaal, but not in Southern Rhodesia. We give only 15 as having their northward range restricted by the Limpopo, but have included only those recorded as far north as the northern Transvaal (in eight cases positively recorded as only extending to the Zoutpansberg). Winterbottom was also at a disadvantage in that the work of Smithers *et al.* (1957) was not available to him when he wrote his paper. He concludes that neither the Limpopo nor Zambezi is an important faunal boundary. To be sure, 67 species out of a total of 497 for the Transvaal not occurring in Southern Rhodesia is only a small proportion. But nevertheless, disregarding such totals, it does seem that the numbers in the lists below are sufficiently high to suggest a considerable significance.

The Limpopo and the Zambezi are referred to as valleys, the remainder of the barriers



SIMPLIFIED VEGETATION MAP OF THE FEDERATION OF THE RHODESIAS & NYASALAND AND PORTUGUESE EAST AFRICA. ADAPTED FROM KEAY *ET AL.* (1959)

THE SIGNIFICANCE OF VALLEYS AS AVIAN ZOOGEOGRAPHICAL BARRIERS

as rifts. According to Dr. G. Bond (*in litt.*), the middle Zambezi has been regarded by some authorities as a rift fault, but it can be shown beyond reasonable doubt that, irrespective of whether it is so or not, very little movement has taken place since the time of the early deposition of Kalahari sand. The surface on which the sand rests in the middle Zambezi has only been tilted about 300 feet in 300 miles since the sand was deposited, and it can be shown that the sand itself rests on an erosion bench, and banks up against a scarp which bounds this bench, not having been faulted by the movements which produced it. In the case of the middle Zambezi, therefore, movements are at least as old as mid-Tertiary. They were therefore much older than the movements already mentioned which occurred in areas further north. Also, according to King (1951: 207), no true rift valleys have been described south of the Sabi, and so, following this author, it is incorrect to refer to the Limpopo Valley as a rift.

The accompanying simplified vegetation map of the Federation largely follows Keay *et al.* (1959). But certain small areas shown by those authors as relatively dry or holding Mopane (types 20 and 22), in plateau country between Livingstone and Broken Hill, have been omitted. The predominant vegetation in this area is *Brachystegia* woodland, and Mopane is relatively scanty. The supposedly relatively dry areas shown between Lake Mweru and the south end of Lake Tanganyika, and west of the south end of Lake Nyasa, have also been omitted. In the former the annual rainfall-average is not less than 40 inches (*fide* map in Brelsford, 1960), with much Itigi thicket (type 12 in Keay *et al.*), while in the latter the average is not less than 32 inches, and the vegetation is mainly *Brachystegia*, at an altitude of not less than 4,000 feet, with some small scattered patches of evergreen forest at over 6,000 feet (Benson, *in litt.*). The dry areas in the littoral of Portuguese territory north of the Zambezi are differentiated from Mopane areas, as indeed they are by Keay *et al.* But it is worth mentioning that Pedro & Barbosa (1955) do not mention *Colophospermum mopane* from this area at all, while Vincent (1934: 149) describes the country behind the mouth of the Lurio River as consisting of park-like thorn scrub.

It will be noticed that, more especially in the Luangwa and Nyasa/Shire lists, various generic names have been added in brackets. This arises from recent changes in nomenclature, in accordance with a broader concept of the genus, rendering in this respect Benson (1953) particularly out of date. The insertion of such names, which have become in effect subgenera, will assist in tracing information referred to.

THE LIMPOPO VALLEY

The low-lying drainage of the Limpopo Valley constitutes a most effective barrier to dispersal. North of the Limpopo River the Southern Rhodesia plateau runs in a north-easterly direction, sloping gradually towards the south-east so that large areas of the country lie below 3,000 feet, and to well below 1,000 feet in the extreme east. Two factors play a part in this region; arid Mopane country predominates from about 28° E., but elsewhere to the west on to the plateau areas of the Bechuanaland Protectorate there is a gradual transition to a wooded steppe with abundant *Acacia* and *Commiphora*; this, accompanied by a faunal change, prevents any southward extension of the plateau avifauna that is elsewhere isolated only by the presence of the ecologically unsuitable valley areas.

The region as a whole contains the most arid country to be found in any of the areas under discussion, the annual rainfall-average being in general less than 16 inches (see map in Brelsford, 1960).

On the South African side of the valley similar conditions prevail until the Transvaal highveld is reached, when one encounters the Zoutpansberg Mountains, reaching an altitude of over 5,000 feet, where true montane forest again makes its appearance, and there are considerable areas of montane grassland (see Keay *et al.*, 1959). This region generally marks the northernmost limit of the typically endemic South African avifauna,

of which only a few constituent species reach the highlands of eastern Southern Rhodesia. There is also a continuation of the low-veld vegetation in the extreme north-eastern Transvaal and the Kruger National Park. Further south, the considerable area of evergreen forest existing at Woodbush marks the southernmost limit of *Malaconotus nigrifrons*, apparently as yet unrecorded from the Zoutpansberg further to the north.

Mention may also be made here of the dry Sabi Rift, where again the annual rainfall-average drops to below 16 inches. But the only evidence of it being a barrier to avian dispersal is in the case of *Psaldoprocne holomelaena*, with which *P. orientalis* has been made conspecific by White (1961). Following Irwin (in press for *Bull. Brit. Orn. Cl.*, 81, 1961), *P. h. holomelaena* occurs on the high ground of the Bikita and Zimbabwe areas west of the Rift, where there is high rainfall, with rich *Brachystegia* woodland and relic evergreen forest. *P. h. orientalis* occurs on the opposite side of the Rift, and in eastern Southern Rhodesia generally, ranging regularly west to Rusape and Inyazura. It has also been recorded south of the Birchenough Bridge on the Sabi River, probably as a wanderer.

The information which follows in regard to the Limpopo Valley acting as a barrier is derived mainly from McLachlan & Liversidge (1957) for the southern side, and Smithers *et al.* (1957, as amended 1959) for the northern side. Attention may be drawn in particular to 15 species frequenting *Brachystegia* woodland on the northern side, but absent on the southern side, where this habitat does not exist. On the other hand several species are mentioned as occurring in this habitat in Southern Rhodesia, but in other types of woodland south of the Limpopo.

A. SPECIES WHOSE RANGE IS RESTRICTED BY THE LIMPOPO VALLEY

(1) *Occurring only on the southern side*

Several of the species in this section occur north of the Zambezi, but are included as they are unknown in Southern Rhodesia.

1. *Geocolaptes olivaceus*: Represents a genus endemic to the Republic of South Africa, frequenting open country, ranging to the northern Transvaal.

2. *Mesopicos griseocephalus*: *M. g. griseocephalus*, associated with evergreen forest, extends as far north as Woodbush (Sclater, 1911). No record has been traced from the Zoutpansberg, where it might also be expected. It does not occur in southern Nyasaland. As indicated by McLachlan and Liversidge (1957). The species is unknown in Southern Rhodesia, possibly due to competition with *Campethera abingoni* (see Smithers *et al.*, 1959). Another subspecies, however, occurs in the north of Northern Rhodesia and Nyasaland (Benson and White, 1961).

3. *Anthus leucophrys*: Although reappearing north of the Zambezi (Zambezi list A (2)), unknown in Southern Rhodesia, but extending from the Cape Province to the northern Transvaal, in open grasslands. Although it occurs in the Sul do Save (Pinto and Lamm, 1953-56), no evidence has been traced of its extensive occurrence in Portuguese East Africa as indicated by McLachlan and Liversidge (1957).

4. *Lioptilus nigricapillus*: Extends north to the Zoutpansberg, inhabiting evergreen forest edges. The genus is also represented in the eastern Congo and Ruanda-Urundi (Chapin, 1953).

5. *Monticola rupestris*; 6. *M. explorator*: Both reach their northern limit in the northern Transvaal, and inhabit open, rocky country.

7. *Oenanthe monticola*: 8. *Myrmecocichla bifasciata*: Both reach their northern limit in the Zoutpansberg and inhabit arid hilly country.

9. *Cossypha dichroa*: Extends north to the Zoutpansberg, in evergreen forest.

10. *Cisticola textrix*: Ranges in open grasslands north to the northern Transvaal;

reappears in the north-west of Northern Rhodesia and in Angola (Benson and White, 1961).

11. *Prinia maculosa*: Finds its northern limit in the Zoutpansberg, inhabiting short bushes in open country.

12. *Spreo bicolor*: Extends in open country to the northern Transvaal.

13. *Nectarinia afra*: Ranges to the northern Transvaal, usually on forest edges. Supposedly conspecific forms occur in eastern Africa, south to the Nyika plateau in northern Nyasaland, and in western Angola, but further investigation is needed as to their true relationship to *N. afra*.

14. *Ploceus capensis*: Extends north to the Zoutpansberg, in almost any type of country where there are trees or bushes, usually near water. Unknown anywhere directly to the north, possibly due to competition with *P. xanthops* (see Benson and White, 1961). It is however represented in Angola and extreme north-western Northern Rhodesia by *P. c. temporalis*.

15. *Serinus scotops*: Extends north to the Zoutpansberg, mostly on the edges of evergreen forest. Specimens of this species and *S. citrinelloides* (see Zambezi list A (2)) have been compared. In plumage they are very similar. The most marked difference is the stouter bill of *S. scotops*, with curved, rather than straight, culmen and keel to lower mandible. In habitat they are apparently analogous. Their relationship is sufficiently close to regard them as at least representing a single superspecies.

(2) *Occurring only on the northern side*

It is convenient to treat the much larger number of species in this section (31) than in (1) above (15) in rough ecological categories.

Brachystegia woodland

1. *Buccandon whytii*: Frequents well developed woodland on the Mashonaland plateau above 3,500 feet, south to Melsetter.

2. *Prodotiscus insignis*: Known from scattered localities above 3,000 feet, from west of the Victoria Falls, as far south as Selukwe in the Midlands, and in the east of Southern Rhodesia.

3. *Campethera cailliautii*: Occurs up to 3,500 feet in rich woodland in the east of Southern Rhodesia, south to Mt. Selinda. There is also a distinct, apparently relic, population at Funhalouro in the Sul do Save (Pinto, 1960).

4. *Hyltiota australis*: Widespread above 3,000 feet in Southern Rhodesia to as far south as the Matopos, but unknown west of about 28° 30'. Also collected in *Acacia xanthophloea* trees at 500 feet at the Sabi/Lundi confluence, and recorded from Coguno in the Sul do Save (Lamm, 1953).

5. *Monticola angolensis*: Throughout Southern Rhodesia above 3,500 feet, occasionally to 2,000 feet.

6. *Sylvietta whytii*: Occurs in eastern Southern Rhodesia as far south as Mt. Selinda, again along the northern fringe of the Mashonaland plateau and south-west to Matabeleland, where it inhabits Baikiaea woodland.

7. *Cisticola brachyptera*: Mostly in secondary growth below 4,000 feet, on the eastern border, south to Chipinga.

8. *Heliolais erythroptera*: Much as for the last species, south to Mt. Selinda.

9. *Parus griseiventris*: Inhabits well developed woodland above 3,500 feet, on the eastern border, south to Mt. Selinda. Unknown further west than about 30° 25'. Although known from Baikiaea woodland at Livingstone (Benson, 1960), it is still unknown from the Southern Rhodesian side in such an association. Regarded as a species distinct from *P. afer* (Hall & Traylor, 1959; Irwin, 1959).

10. *Parus rufiventris*: Distribution in Southern Rhodesia as for the last species, though occurs as low as 2,000 feet.

11. *Lamprotornis chloropterus*: General, except that apparently only a seasonal wanderer to southern Matabeleland. Recorded as far south as the mouth of the Save (Pinto & Lamm, 1956).

12. *Anthreptes longuemarei*: Throughout the eastern border, where it occurs down to 2,000 feet in rich woodland. Elsewhere on the plateau only usually above 3,500 feet, and unknown west of 30° 25'.

13. *Salpornis spilonta*: Restricted to rich woodland on the plateau as far south as the Selukwe District and Bikita above 3,000 feet, but unknown west of the Sengwa River, and not so far recorded on the eastern border.

14. *Serinus mennelli*: Occurs on the plateau above 3,000 feet in Baikiaea as well as Brachystegia woodland, just reaching Bechuanaland at Panda Matenga (Hall, 1956). In eastern Southern Rhodesia, found as low as 2,000 feet.

15. *Emberiza cabanisi*: Ranges in rich woodland as far south as the Midlands, and in the east to Melsetter, usually above 3,000 feet, though lower in the east.

It is worth mentioning that the following species, characteristic of Brachystegia woodland in Southern Rhodesia, nevertheless occur in other types of woodland south of the Limpopo:—*Anthus similis*, *A. lineiventris*, *Coracina pectoralis*, *Eremomela scotops*, *Cisticola aberrans*, *Nectarinia chalybea* and *Serinus gularis*. However, *Anthus lineiventris* and *Cisticola aberrans* are essentially associated with a rocky habitat both to the north and south of the Limpopo. *Coracina pectoralis* and *Eremomela scotops* have in fact both also been found associated with *Acacia xanthophloea* trees at the Sabi/Lundi confluence, and recently Irwin has found *Eremomela scotops* common alongside *E. usticollis* in alluvial Acacia growth on the lower Nuanetsi River at 22° 02'S., 31° 25' E., seemingly replacing *E. icteropygialis*.

Evergreen forest

All seven of the following species are confined in Southern Rhodesia to the eastern border.

16. *Bycanistes brevis*: South to Mt. Selinda, between 2,000 and 7,000 feet.

17. *Andropadus milanensis*: General between 2,000 and 7,000 feet.

18. *Trochocercus albonotatus*: Represented in this area by an endemic subspecies, ranging from 3,500 to 7,000 feet.

19. *Pogonocichla swynnertoni*: A distinctive endemic species, ranging from 3,000 to 5,000 feet.

20. *Apalis (melanocephala) chirindensis*: Usually regarded as conspecific with *A. melanocephala*, but perhaps best treated as an endemic species, probably overlapping with the distinctly coloured *A. m. lightoni* at the southern end of the Chimanimani Mts. *A. (m.) chirindensis* occurs between 2,000 and 7,000 feet.

21. *Prinia robertsi*: A distinctive endemic species, common between 4,000 and 7,000 feet, mostly on forest edges and in secondary growth.

22. *Cryptospiza reichenovii*: Between 4,000 and 7,500 feet. Certain lowland species, none of which occur higher than 2,000 feet in eastern Southern Rhodesia, are not formally included. These are *Phyllastrephus debilis* and *Bias musicus*, extending south in Portuguese East Africa to Inhambane; and *Prionops scopifrons* and *Pirenestes minor*, south to Beira. For particulars of the distribution of *Apalis melanocephala lightoni*, see Zambezi list B.

Miscellaneous

23. *Apus myoptilus*: Known from cliff-faces at Inyanga and on the Chimanimani Mts.

23a. *Apus aequatorialis*: Frequents cliff-faces as far south as Mashonaland and eastern Southern Rhodesia, wandering as far south as Bulawayo.

24. *Pinarornis plumosus*: Ranges from Fort Jameson and Petauke, in Northern Rhodesia, south-west to Bulawayo, in association with rocky kopjes. The record from the Percy Fyfe Nature Reserve, south of the Limpopo (van der Merwe and Pienaar, 1959), cannot be accepted.

25. *Cisticola cantans*: Inhabits bracken growth, south to Mt. Selinda, west to Rusape. Specimens from Selukwe, on the basis of which it was recorded by Smithers *et al.* (1957), are actually attributable to *C. aberrans*, nor has its occurrence at Salisbury been substantiated (C. J. Vernon, *in litt.*).

26. *Sphenoeacus (Melocichla) mentalis*: In Southern Rhodesia, confined to the eastern border below 3,500 feet, south to Mt. Selinda, inhabiting rank grass growth near streams. Generic name in accordance with White (1960d).

27. *Tchagra minuta*: Range and habitat similar to that for the last speciss.

28. *Nectarinia kilimensis*: In Southern Rhodesia, confined to the eastern border above 4,500 feet, mainly in bracken growth on the edge of evergreen forest.

29. *Nectarinia venusta*: Disregarding a population in the Zambezi Valley, confined in Southern Rhodesia to the eastern border; unknown west of Macheke, ranging from 1,000 to 7,500 feet, habitat as for the last species.

30. *Euplectes hordeaceus*: Ranges south to Mt. Selinda, extending west to Inyazura. Inhabits rank grass with herbaceous growth below 4,000 feet.

31. *Euplectes macrourus*: Inhabits wet short grasslands on the Mashonaland plateau to as far south as Selukwe and Chatsworth.

32. *Oryzospiza locustella*: Habitat and distribution similar to that for the last species.

B. SUBSPECIFIC DIFFERENCES ON THE TWO SIDES OF THE VALLEY

1. *Tauraco persa* (= *T. corythaix*): A population akin to *T. p. corythaix*, but not identical, occurs as far north as the Zoutpansberg. In eastern Southern Rhodesia it is replaced by *T. p. livingstonii*. Habitat evergreen forest and dense thickets. For further details, see Moreau (1958).

2. *Batis capensis*: An evergreen forest species; *B. c. capensis* north to the Zoutpansberg, *B. c. erythrophthalma* in eastern Southern Rhodesia.

3. *Turdus olivaceus*: Habitat as for the last; *T. o. transvaalensis* in the northern Transvaal, *T. o. swynnertoni* in eastern Southern Rhodesia.

4. *Phylloscopus ruficapilla*: Habitat as for the last; *P. r. johnstoni* in eastern Southern Rhodesia, *P. r. ruficapilla* in the Zoutpansberg.

5. *Bradypterus barratti*: Habitat as for the last; *B. b. barratti* in the northern Transvaal, *B. b. priestii* in eastern Southern Rhodesia.

6. *Apalis thoracica*: Associated with evergreen forest and thickets; *A. t. spelonkensis* in the Zoutpansberg, *A. t. arnoldi* in eastern Southern Rhodesia, *A. t. rhodesiae* further west.

7. *Cisticola aberrans*: Apparently always associated with rocks (see also above); *C. a. aberrans* in the Transvaal, *C. a. nyika* in Southern Rhodesia.

8. *Hirundo fuligula*: Associated with rock-faces; *H. f. fuligula* in the Transvaal, *H. f. fusciventris* in Southern Rhodesia (and northwards across the Zambezi Valley, which forms no such marked barrier as the Limpopo; note that *H. f. rufigula* in Benson, 1953 is the same as *H. f. fusciventris*, following White, 1957).

9. *Malacotus olivaceus*: An evergreen forest species; *M. o. olivaceus* in the northern Transvaal, *M. o. makawa* in eastern Southern Rhodesia.

10. *Nectarinia chalybea*: *N. c. subalaris* in the Transvaal, with apparently no marked habitat preference; *N. c. manoensis* in Southern Rhodesia, more especially in *Brachystegia* woodland.

11. *Promerops gurneyi*: Associated with *Protea* bushes; *P. g. gurneyi* in the northern Transvaal, *P. g. ardens* in eastern Southern Rhodesia.

12. *Lagonosticta rubricata*: Commonly in bracken growth on the edge of the evergreen forest; *L. r. rubricata* in the northern Transvaal, *L. r. haematocephala* in eastern Southern Rhodesia.

13. *Serinus sulphuratus*: Habitat not clearly definable, but often near water; *S. s. wilsoni* in the Transvaal, *S. s. sharpii* in eastern Southern Rhodesia.

14. *Fringillaria capensis*: A rock-dweller; *F. c. limpopoensis* in the Zoutpansberg, *F. c. plowesi* in Southern Rhodesia, replaced by *F. c. smithersii* in the Chimanmani Mts. For a discussion of the phylogeny of the various more northern subspecies, see Irwin (1958).

15. *Estrilda melanotis*: edge of evergreen forest and rank growth. *E. m. melanotis* ranges as far north as the Zoutpansberg, in eastern Southern Rhodesia it is replaced by the very different *E. m. kilimensis*. A black-faced form similar to that found in South Africa has once been recorded from the Matopos, but its status as a wild population seems to be in some doubt.

16. *Sarothrura a. affinis* has been recorded from the eastern Cape Province, *S. a. antonii* from eastern Southern Rhodesia. It is not included above because there are apparently still no records of either from the Transvaal.

To this list must be added *Buteo rufofuscus*: Inhabits mountainous or hilly country; *B. r. rufofuscus* ranges as far north as the Zoutpansberg and also to northern South West Africa. *B. r. augur* on the other hand replaces it northwards from the plateau of Southern Rhodesia to Abyssinia.

THE ZAMBEZI VALLEY

The sector for consideration is that between the Victoria Falls and the Indian Ocean. It is convenient to divide it into two sub-sectors and to treat them separately:—

- (a) Above Chemba, on the river at about 35° E.; generally a well marked escarpment on either side of the valley; conditions relatively arid, Mopane woodland predominating.
- (b) Below Chemba, escarpment not so well marked, while towards the entrance of the river to the sea there are hundreds of miles of country below 600 feet, both to the north and south; conditions more humid, *Brachystegia* replacing Mopane.

Considering sub-sector (a), for some 60 miles below the Falls the Zambezi flows through narrow rocky gorges, below which a valley floor fans out, as much as 30 miles across in places. The general altitude of the floor in the upper reaches is about 1,300 feet, gradually descending to less than 600 feet near Tete. For the most part there is a well marked escarpment on either side of the valley, the top of which is 2,000–3,000 feet above the floor. Various rivers cut through the escarpment, such as the Gwaai and the Sanyati on the southern side, while much the most important on the northern side is the Luangwa.

The annual rainfall-average between the Victoria Falls and Kariba is 16–24 inches, between Kariba and Chicowa 24–32, dropping again around Tete to 16–24, rising again towards Chemba to 24–32. The figures for plateau country on either side above the valley average higher. North of the area between the Victoria Falls and Chirundu a 32–40 inch isohyet is attained, and near Furancungo (north of Tete) even 48–56.

The characteristic vegetation of the valley is Mopane woodland, intersected by alluvial *Acacia* growth. But there are also extensive areas of dense thicket, particularly well developed between Kariba and Chirundu. The vegetation is in general contrast to that on the plateau country on either side, where *Brachystegia* woodland predominates. However, there is Mopane on the plateau in the arid west of Southern Rhodesia, and likewise in relatively small scattered pockets in the Southern Province of Northern Rhodesia. Here, such birds as *Tockus erythrorhynchus*, *Lamprotornis mevesii* and *Plocepasser mahali*, so characteristic of the valley, are liable to occur.

At Kariba, relatively high ground, rising to over 2,500 feet, closes in on the river gorge. The vegetation is *Brachystegia* woodland, as in plateau country. Although these hills have not been worked ornithologically, their avifauna is probably rather depauperate, with many typical plateau *Brachystegia* species absent.

Considering sub-sector (b), the contrast to (a) is marked. Towards the coast there is a broad belt of country where the annual rainfall-average does not drop below 40 inches, while north and south of the Zambezi mouth it rises to 48 inches, and at Beira the isohyet is even 56-64 inches. This increase in humidity is reflected in the vegetation. According to Pedro & Barbosa (1955), Mopane woodland does not extend appreciably further east than Chemba, and there is a practically continuous belt of *Brachystegia*, from eastern Southern Rhodesia through the coastal littoral to Mlanje, in southern Nyasaland. Between Beira and the Zambezi mouth, too, there are even pockets of evergreen forest, judging from some of the trees listed by these authors.

The foregoing is derived from:—Anon. (1960); Brelsford (1960) (rainfall-map); Pedro & Barbosa (1955); Trapnell *et al.* (1948); and Trapnell & Clothier (1957). The lists of birds below to which the Zambezi Valley acts as a barrier have been obtained mainly from Benson (1953); Benson & White (1957); Smithers *et al.* (1957, as amended 1959); and Vincent (1933-36). Any specimens particularly mentioned are in the National Museum, Bulawayo.

Before proceeding to these lists, however, some discussion is necessary as to the possibility of a connection above the Victoria Falls or through the humid sea-littoral. At the end of list B below (subspecific differences) there is a further list of species showing no differentiation on the two sides of the valley even though there is no evidence of any gene-flow. On the other hand, some species which are generally absent below the Falls do link up above, through an area of poorly developed *Brachystegia* as well as *Baikiaea* woodland. In Southern Rhodesia and the Southern Province of Northern Rhodesia, the more specialised *Brachystegia* species do not range as far west as the Falls, on either side of the Zambezi. But examples of those which do are *Anthus similis*, *Coracina pectoralis*, *Bradornis pallidus*, *Eremomela icteropygialis*, *E. scotops*, *Camaroptera stierlingi*, *Cisticola fulvicapilla* (recent study shows the populations of Southern Rhodesia and the south of Northern Rhodesia to be very similar, with *C. f. hallae* extending from the Falls westwards), *Anthoscopus caroli* (with the qualification that recently a specimen apparently representing a distinct subspecies has been collected at Feira), and *Serinus mennelli*. Examples from other habitats are *Lanius melanoleucus* (excepting a record by Benson & White, 1957: 161) and *Ortygospiza atricollis*.

With regard to the possibility of a connection through the humid sea-littoral between eastern Southern Rhodesia and Mlanje, in southern Nyasaland east of the Nyasa/Shire Rift, in list B below there is the case of *Apalis melanocephala lightoni* among evergreen forest forms, while the populations of *Andropadus m. milanensis* could have been linked up in a colder climate (there is no evidence of any link at the present time). Among *Brachystegia* forms, under colder conditions there could have been a link between the populations, apparently now separated, of *Parus rufiventris pallidiventris* and *Anthreptes longuemareae nyassae*. On the other hand, this does not explain, for example, the case of *Buccanodon whytii sowerbyi* or *Apalis thoracica arnoldi*, for which it seems necessary to postulate a link further up the valley, where Mopane now predominates. To take another type of example, *Parus griseiventris*, in which no subspecies are recognized, at the present time is confined in Southern Rhodesia to the eastern part, but occurs in Northern Rhodesia as far south as Livingstone (Limpopo list A(2)). In Nyasaland it is only known on the west of the Nyasa/Shire Rift. In this case it seems necessary to postulate a connection between eastern Southern Rhodesia and Livingstone under more humid conditions.

A. SPECIES WHOSE RANGE IS RESTRICTED BY THE ZAMBEZI VALLEY

(1) *Occurring only on the southern side*

1. *Columba guinea*: Widespread on rocky hills in Southern Rhodesia. Although it reappears in eastern Africa, to as far south as the Rukwa Valley (Vesey-Fitzgerald & Beesley, 1960), it is unknown in Northern Rhodesia, Nyasaland or Portuguese East Africa north of the Zambezi.

2. *Macronyx capensis*: Inhabits wet grasslands above 3,000 feet in Southern Rhodesia, but unknown further north. Incidentally, it occurs throughout the Inyanga area above 4,000 feet, but is replaced below this level by *M. croceus*. At Chimanimani only the latter is found, occurring up to 6,000 feet, and as low as 500 feet at the Sabi-Lundi confluence.

3. *Bessonornis humeralis*: The northernmost limit of the range is the top of the southern escarpment of the Zambezi Valley. A thicket-dweller, widespread in Southern Rhodesia.

4. *Sphenoeacus afer*: Unknown north of Inyanga. Confined in Southern Rhodesia to the east of the territory, typically inhabiting rank bracken growth.

5. *Eurocephalus anguitimens*: Typically, inhabits thorn country and Brachystegia edges on the plateau of Southern Rhodesia (*E. a. anguitimens*), but unknown north of the Zambezi south of the Rukwa Valley (Vesey-Fitzgerald & Beesley, 1960), where the form is presumably *E. a. ruppelli*.

6. *Promerops gurneyi*: Unknown north of eastern Southern Rhodesia, where associated with Protea bushes. *P. g. ardens* is endemic to this area.

Mention has already been made of *Pogonochla swynnertoni* and *Prinia robertsi*, endemic to the evergreen forests of eastern Southern Rhodesia. *Apalis (melanocephala) chirindensis* (see also under list of subspecific differences), is another endemic, so distinct and occurring so close to *A. m. lightoni*, that it is perhaps also best regarded as a species. They will probably prove to overlap at the south end of the Chimanimani Mts. between 1,000 and 2,000 feet.

(2) *Occurring only on the northern side*

It is convenient to treat the much larger number of species in this section (35) than in (1) above (8) in rough ecological categories.

Brachystegia woodland

The following list could be increased considerably by the inclusion of various further species widespread in the north of Northern Rhodesia and in some cases in Nyasaland as well. But as none of them occur south of 14°, and so do not approach at all closely the low lying ground of the Zambezi their inclusion is not appropriate. It is particularly noteworthy that there is not a single Brachystegia species occurring in Southern Rhodesia which is not represented to the north of the Zambezi.

1. *Tockus pallidirostris*: In Southern Nyasaland to the Port Herald District (Long, 1960-61); in Northern Rhodesia to as far south as Rufunsa, the Kafue River at 15° 50' S., 28° 20' E. (recent specimen), though unknown in the Southern Province.

2. *Ipophilus stierlingi*: Occurs near the southern extremity of the Nyasa/Shire Rift on both sides, in Nyasaland, and in Portuguese East Africa (Vincent, 1933-36).

3. *Muscicapa (Myopornis) boehmi*: See Nyasa/Shire list A (1), though west of the Luangwa Rift unknown south of Broken Hill.

4. *Hylia flavigaster*: An excellent example, occurring extensively on both sides of the Nyasa/Shire Rift, and in Northern Rhodesia collected as far south as the Kalomo District (Benson, 1958), and recently on the lip of the escarpment in the Choma District at 17° 00' S., 27° 20' E.

5. *Elminia albicauda* (—*Erannornis longicauda*): See Nyasa/Shire list A (1), though west of the Luangwa Rift unknown south of about 14°.

6. *Erythropygia barbata*: See Nyasa/Shire List A (1), but west of the Luangwa Rift unknown south of 14° 40' (Benson *et al.*, 1959).

7. *Sylvietta ruficapilla*: See Nyasa/Shire List A (1), while west of the Luangwa Rift collected in the Kalomo District (Benson, 1958) and recently on the lip of the escarpment in the Choma District, at 17° 00' S., 27° 20' E. An excellent example.

8. *Lanius souzai*: Present near the southern extremity of the Nyasa/Shire Rift on both sides. West of the Luangwa Rift, extends as far south as Lusaka and the Sesheke District, but unknown in the Southern Province (Benson, 1959). The statement by Vincent (1952) that it occurs in the "mid-Zambezi valley" appears to be based on his record (1935) from Furancungo in plateau country well north of the valley.

9. *Nectarinia shelleyi*: The type-locality of *N. s. shelleyi* is from the Zambezi Valley, whence there is no subsequent record. The two specimens collected by Alexander may have been wanderers from plateau country to the northward. The species occurs uncommonly on both sides of the Nyasa/Shire Rift, and in Northern Rhodesia south to Kalomo and Livingstone.

10. *Antheptes anchietae*: See Nyasa/Shire List A (1); though west of the Luangwa Rift unknown south of Broken Hill.

11. *Ploceus (Phormoplectes) olivaceiceps*: Present on both sides of the Nyasa/Shire Rift, but unknown south of the Zambezi, except that Clancey (*in litt.*) has recently obtained it at Panda in the Sul do Save.

Mention should also be made of *Lybius leucomelas frontatus*, which it is in fact perhaps arguable is a distinct species. This particular form inhabits Brachystegia, whereas all other forms prefer by contrast thornveld. *L. l. frontatus* and *L. l. centralis* show evidence of secondary hybridization rather than clinal intergradation near Livingstone (Benson & White, 1961). Typical *L. l. frontatus* is widespread in Northern Rhodesia west of the Luangwa Rift and three specimens of it have recently been collected near Choma at 16° 39' S., 27° 01' E. For the position further east see Nyasa/Shire List A (1).

Evergreen forest

All the species in this list extend into southern Nyasaland, and with the exception of *Phyllastrephus cerviniventris* none of them occur in Northern Rhodesia except in certain cases in the north. The last three on the list inhabit forest edges rather than the interior.

12. *Apaloderma (Heterotrogon) vittata*: Extends as far south in Nyasaland as Cholo and Mlanje, and in Portuguese East Africa at Namuli.

13. *Pogoniulus (Viridibucco) leucomystax/simplex*: See Nyasa/Shire List B.

14. *Indicator meliphilus*: Occurs on both sides of the Nyasa/Shire Rift, even as far south as Malawi (Long, 1960–61).

15. *Phyllastrephus cerviniventris*: Extends into southern Nyasaland on both sides of the Rift, and in Northern Rhodesia as far south as Chilanga (Benson and White, 1957: 160), mainly in riparian growth.

16. *Phyllastrephus fischeri*: *P. f. placidus* occurs in Nyasaland as far south as Mlanje.

17. *Andropadus (Arizelocichla) tephrolaema*: As for the last species.

18. *Andropadus (Eurillas) virens*: Occurs in Nyasaland as far south as Cholo (Vincent, 1935).

19. *Alethe choloensis*: As far south as Cholo, and Chiperoni (Benson, 1950).

20. *Bessonornis anomala*: See Nyasa/Shire list B.

21. *Apalis chariessa*: See Nyasa/Shire list A (2).

22. *Apalis porphyrolaema*: See Nyasa/Shire list A (1).

23. *Oriolus chlorocephalus*: See Nyasa/Shire list A (2).
 24. *Nectarinia mediocris*: South in Nyasaland to the Kirk Range and Mlanje, mostly on forest edges.
 25. *Ploceus (Xanthoploceus) bertrandi*: Extends into southern Nyasaland on both sides of the Rift, almost entirely on forest edges.
 26. *Serinus (Carduelis) citrinelloides*: As for the last species, mostly in bracken growth on the edge of forest. Closely allied to *S. scotops*, see Limpopo List A (1).

Miscellaneous—mainly swamps and open grasslands

27. *Centropus cupreicaudus*: Widespread in Northern Rhodesia in swamps west of the Luangwa Rift, extending into the Caprivi, northern Bechuanaland and probably into Southern Rhodesia, but only in the extreme north-west.
 28. *Anthus leucophrys*: In Northern Rhodesia west of the Luangwa Rift, extends in open grasslands throughout Barotseland, into northern Bechuanaland (Benson and White, 1961). Recently collected on the south side of the Kafue Flats at 15°50' S., 27°05' E., and see Nyasa/Shire List A (1). It reappears in the Transvaal and the Sul do Save, but is unknown in Southern Rhodesia.
 29. *Macronyx fulleborni*: Inhabits wet grasslands in the greater part of Northern Rhodesia west of the Luangwa Rift, extending into Barotseland and plateau country in the Southern Province, but unknown any further south. In Southern Rhodesia it is replaced by the ecologically very similar *M. croceus* and *M. capensis*.
 30. *Turdoides leucopygia*: Distribution similar to the last, but extending into northern Bechuanaland. Habitat open grasslands with scattered low bushes.
 31. *Parusoma lugens*: See Nyasa/Shire list A (1).
 32. *Myrmecocichla nigra*: Inhabits dry grasslands in Northern Rhodesia west of the Luangwa Rift, extending into Barotseland and plateau country in the Southern Province.
 33. *Hirundo daurica*: This species is unknown south of the southern end of the Nyasa/Shire Rift, where it is found on both sides, on rocky hills.
 34. *Parus leucomelas*: See Nyasa/Shire list A (1). In Northern Rhodesia west of the Luangwa Rift, extends south to Mazabuka.
 35. *Lagonosticta rufopicta*: See Luangwa list A (1). Recorded from the Kafue Gorge (Benson, 1959), and extends through Barotseland to the extreme north-west of Southern Rhodesia.

Exclusive of the above lists, it should be mentioned that *Cercocoryx montanus* extends in dense thickets into the extreme south of Nyasaland. The same also applies to *Merops boehmi*. McLachlan & Liversidge (1957) include the latter, but Pinto (*in litt.*) has no evidence of its occurrence in Portuguese territory south of the Zambezi, and Smithers *et al.* (1957) positively reject it for Southern Rhodesia. In any case, neither species can be formally included above, since they both occur in southern Nyasaland as low as 200 feet.

B. SUBSPECIFIC DIFFERENCES ON THE TWO SIDES OF THE VALLEY

It is also convenient to include here one species-pair, *Turdus olivaceus abyssinicus*. There are a number of very anomalous and puzzling cases in this section. It would be expected that the narrower Nyasa/Shire Rift (especially the Shire section) would be of little significance compared to the Zambezi Valley. Yet one finds the same subspecies of *Tauraco persa* in eastern Southern Rhodesia and east of the Nyasa/Shire Rift, but another to the west. Conversely, the same subspecies of *Cisticola aberrans* occurs in Southern Rhodesia and west of the Nyasa/Shire Rift, another to the east. If the affinities of the Southern Rhodesian subspecies were always with one side or other of the Nyasa/Shire Rift in those

cases in which there is a difference on the two sides of this area, the situation would be susceptible of an explanation, but this is not so. Particular attention should be drawn to the cases of *Buccanodon whytii*, *Andropadus milanensis*, and *Apalis melanoccephala*, which present even further complications. That of *Apalis thoracica*, represented by an unusually richly coloured subspecies at Mlanje and Zomba, is also most remarkable. On the other hand, the cases of *Batis capensis*, *Trochocercus albonotatus*, *Pogonocichla stellata*, and various others, in which there is one subspecies in Southern Rhodesia, another on both sides of the Nyasa/Shire Rift, seem quite straightforward, according to expectation. In *Parus rufiventris*, attention may be drawn to the start of a cline in the area west of the Nyasa/Shire Rift and at Chilanga, Northern Rhodesia, but interrupted by the Valley.

1. *Tauraco persa* (—*T. corythaix*): *T. p. livingstonii* occurs in eastern Southern Rhodesia, and is separated in the Zambezi Valley below the Victoria Falls from northern populations by the competing *T. porphyreolophus*. In Northern Rhodesia and in Nyasaland west of the Nyasa/Shire Rift there occurs *T. p. schalowi*, with the anomaly that to the east of the Rift *T. p. livingstonii* reappears. *T. p. schalowi* only crosses the Zambezi above the Falls at Namipini. This species inhabits evergreen forest and dense thickets. For further details, see Moreau (1958).

2. *Buccanodon whytii*: Mainly a *Brachystegia* woodland species. *B. w. irwini* occurs in the east of Southern Rhodesia, but is replaced in the north-east by *B. w. sowerbyi*, which reappears in plateau country between the Nyasa/Shire and Luangwa Rifts, but is represented to the east of the former by *B. w. whytii*. The anomalous situation of two apparently distinct subspecies in Southern Rhodesia, where there is no zoogeographical barrier, with *B. w. sowerbyi* reappearing to the north of the Zambezi, requires further investigation.

3. *Motacilla capensis*: *M. c. simplicissima* is widespread in swamps in Northern Rhodesia west of the Luangwa Rift, extending into the Caprivi. But records from the Zambezi Valley are rejected by Benson (1959), while a specimen recorded by Irwin (1956) as *M. c. beirensis* has been re-examined by him and found to be a juvenile *M. aguimp*. In Southern Rhodesia the subspecies is *M. c. capensis*. For a recent revision, see Winterbottom (1959b).

4. *Andropadus milanensis*: An evergreen forest species, represented in eastern Southern Rhodesia by *A. m. milanensis*. On both sides of the Nyasa/Shire Rift, to as far east as Cholo, Blantyre and Zomba, the easily distinguishable *A. m. olivaceiceps* (see Rand, in Mayr & Greenway, 1960) occurs. And yet at Mlanje there is the anomaly that *A. m. milanensis* reappears, extending east to Chiperoni and Namuli. Cholo and Mlanje are little more than 20 miles apart, with intervening riparian forest, if not now destroyed in interests of agriculture.

5. *Phyllastrephus flavostriatus*: Another evergreen forest species, represented in eastern Southern Rhodesia by *P. f. flavostriatus*, in Nyasaland and Portuguese East Africa to the east of the Rift by *P. f. vincenti*, to the west by *P. f. alfredi*.

6. *Coracina caesia*: Habitat as for the last. *C. c. caesia* in eastern Southern Rhodesia, *C. c. pura* in southern Nyasaland, to the east of the Rift, also near Malawi (Long, 1959), and Chiperoni (Benson, 1950).

7. *Hyliota australis*: A *Brachystegia* woodland species. *H. a. australis*, as in Southern Rhodesia, is recorded by Benson & White (1957) from the greater part of Northern Rhodesia. Of material in the National Museum, Bulawayo, 13 adult males from Northern Rhodesia (six from the Southern Province, three from the Northern Province, four from the North-Western Province) are rather more intensely black above, less intensely washed with buff below, than in 17 from Southern Rhodesia. No such analogous differences are discernible in females, of which four have been available from Northern Rhodesia (two from the Southern Province, one from the Central Province, one from the North-Western Province), and 14 from Southern Rhodesia. Reference variation in the pattern of the outer pair of tail-feathers,

discussed by White (1957) and Hall (1960), the specimens from the Northern and North-Western Provinces lack any white. The remainder all show a variable amount of white. Birds from the southern part of Northern Rhodesia may be referable to *H. a. inornata*, described from east of the Luangwa Rift (no specimens from that area have been available), but in any case they are not identical with *H. a. australis*.

8. *Batis capensis*: Habitat evergreen forest. *B. c. erythrophthalma* in eastern Southern Rhodesia, *B. c. dimorpha* in southern Nyasaland and Portuguese territory on both sides of the Rift.

9. *Trochocercus albonotatus*: Habitat as for the last. *T. a. swynnertoni* in eastern Southern Rhodesia, *T. a. albonotatus* in southern Nyasaland and Portuguese territory on both sides of the Rift.

10. *Turdus olivaceus abyssinicus*: *T. o. swynnertoni* occurs in evergreen forest in eastern Southern Rhodesia, being replaced in southern Nyasaland on both sides of the Rift by the analogous and closely allied *T. abyssinicus milanjensis* (regarded as a different species, following Chapin, 1953). *T. olivaceus* reappears in the north of Northern Rhodesia, west of the Luangwa Rift, as *T. o. stormsi*.

11. *Thamnodula cinnamomeiventris*: A rock-frequenting species, represented south of the Zambezi by *T. c. cinnamomeiventris*, to the north by *T. c. subrufipennis*. The occurrence of the former at the Victoria Falls (Benson & White, 1957) has not so far been substantiated.

12. *Pogonocichla stellata*: An evergreen forest species. *P. s. transvaalensis* in eastern Southern Rhodesia, *P. s. orientalis* on both sides of the Rift in southern Nyasaland and Portuguese East Africa. See especially Moreau (1951).

13. *Bradypterus baboecala*: A swamp-dweller, represented by *B. b. baboecala* in Southern Rhodesia, by *B. b. moreaui* in Nyasaland and eastern Northern Rhodesia. Western Northern Rhodesia, the Caprivi and northern Bechuanaland are inhabited by *B. b. msiri*. See White (1960d).

14. *Bradypterus barratti*: *B. b. priesti* occurs in eastern Southern Rhodesia, in and around the edges of evergreen forest. It is replaced in southern Nyasaland by *B. b. granti* (*Sathrocercus mariae* in Benson, 1953, the nomenclature here adopted being that of White, 1960d).

15. *Apalis thoracica*: *A. t. whitei* of southern Nyasaland west of the Nyasa/Shire Rift is considered by White (1960c) a synonym of *A. t. arnoldi* of eastern Southern Rhodesia. Yet on the east of the Rift there is the very distinct *A. t. flavigularis*. See further under Nyasa/Shire list B.

16. *Apalis melanocephala*: In evergreen forest in the highlands of eastern Southern Rhodesia there occurs the very distinct *A. (m.) chirindensis*. Near the confluence of the Haroni and Lusitu Rivers, at the southern end of the Chimanimani Mts., *A. m. lightoni* occurs, also found at Beira, and again in southern Nyasaland on the east of the Rift from Blantyre northwards, but with intervening forests at Mlanje and Cholo occupied by *A. m. fuliginosa*.

17. *Eremomela scotops*: Frequents mainly *Brachystegia* woodland, generally rare or absent from low levels. In Southern Rhodesia it is represented by *E. s. scotops*, reappearing on the eastern side of the Nyasa/Shire Rift, except at Matindi, north of Blantyre, where it is replaced by *E. s. pulchra*. *E. s. pulchra* is the form west of the Rift, and in Northern Rhodesia, intergrading with *E. s. scotops* in north-eastern Matabeleland (Smithers *et al.*, 1959), the Zambezi above the Victoria Falls forming no barrier.

18. *Camaroptera stierlingi*: Mainly a *Brachystegia* woodland species. According to Irwin (1960), Southern Rhodesia is inhabited by *C. s. irwini*, extending across the Zambezi above the Victoria Falls into the Livingstone and Kalomo Districts of Northern Rhodesia (recent specimens are also available from the Choma District), but is replaced further north by *C. s. butoni*. *C. s. irwini* reappears in plateau country between the Luangwa and Nyasa/Shire Rifts, while east of the latter *C. s. stierlingi* occurs. Irwin records *C. s. butoni* from the

Gwembe Valley. Actually the specimen on which this is based (see also Benson, 1960a) was collected on the lip of the escarpment at an altitude of 4,000 feet. There appear to be no records from the Zambezi Valley proper, which makes it difficult to explain the reappearance of *C. s. irwini* in eastern Northern Rhodesia and western Nyasaland. However, it may be that it extends across the valley sparsely, and has so far been overlooked. Benson (1953) gives a few records of the species from within the Nyasa/Shire Rift.

19. *Cisticola brunneus*: In Mashonaland represented in wet short grasslands by a population regarded as intermediate between *C. b. egregia* and *C. b. cinnamomea*. Northern Rhodesia west of the Luangwa Rift to as far south as Broken Hill (Benson, 1959), the Busanga Swamp (recent specimens) and Luete are inhabited by *C. b. cinnamomea*.

20. *Cisticola lais*: In montane short grasslands in eastern Southern Rhodesia, *C. l. mashona*; replaced on both sides of the Nyasa/Shire Rift in southern Nyasaland by *C. l. semifasciata*.

21. *Cisticola tinniens*: *C. t. tinniens* occurs in swamps in Southern Rhodesia, while *C. t. shiwa* extends south in Northern Rhodesia to the Mkushi River (Benson, 1959).

22. *Cisticola aberrans*: *C. a. nyika* is widespread in scattered rocky localities, usually in Brachystegia woodland, in Southern and Northern Rhodesia, and Nyasaland west of the Nyasa/Shire Rift, but is replaced to the east by *C. a. lurio* (regarded by White, 1960b, as conspecific with *C. aberrans*).

23. *Lanius collaris*: Open grassy areas with scattered bushes above 3,000 feet in Southern Rhodesia are inhabited by *L. c. subcoronatus* and *L. c. predator*. In Northern Rhodesia the species is represented by *L. c. capelli*, and is generally absent from lower levels (Benson, 1959). This subspecies extends at least as far south as the Choma and Sesheke Districts (Benson, *op. cit.* and 1960b). For the position in Nyasaland, see Nyasa/Shire Rift list B.

24. *Malaconotus olivaceus*: An evergreen forest species, represented by *M. o. makawa* in eastern Southern Rhodesia and southern Nyasaland west of the Nyasa/Shire Rift, but by *M. o. bertrandi* to the east.

25. *Parus rufiventris*: A very anomalous case. *P. r. pallidiventris* occurs in north-eastern Southern Rhodesia south to Mt. Selinda, in Brachystegia woodland. It reappears to the east of the Nyasa/Shire Rift, but is represented to the west by *P. r. masukuensis*, except that from Zobue, *P. r. pallidiventris* has been recorded (Vincent, 1935), while specimens from Fort Jameson incline towards the latter. The Zobue specimen has been re-examined by Mrs. B. P. Hall, from whose report however it is evidently only slightly paler rufous on the belly than in specimens of *P. r. masukuensis*, and accordingly closer to that form, while a specimen from Pirilongwe is evidently intermediate. In Northern Rhodesia west of the Luangwa Rift, *P. r. masukuensis* ranges south to near the lip of the escarpment at Chilanga, though a series of eight specimens from this locality actually show slight signs of intergradation with *P. r. pallidiventris*, being rather paler on the belly than in *P. r. masukuensis*.

26. *Nectarinia chalybea*: Mainly a Brachystegia woodland species. The populations of Southern and Northern Rhodesia are quite easily distinguishable, the former as *N. c. bractiata*, the latter as *N. c. intermedia* (Benson & White, 1957: 162). *N. c. intermedia* extends as far south as the Kalomo District (Benson, 1959) and has recently been collected in the Choma District on the tip of the escarpment at 17°00' S, 27°20' E. According to Macdonald (1958), *N. c. bractiata* is a synonym of *N. c. manoensis*, which is the form in southern Nyasaland. Macdonald gives the Luangwa as the dividing line between *N. c. intermedia* and *N. c. bractiata*, whereas Benson & White place all Northern Rhodesian birds with *N. c. intermedia*. The problem requires further investigation, but it appears that the Zambezi Valley acts as a subspecific barrier at least in the sector between the Victoria Falls and Feira, but not so further east, even though there is no evidence of the occurrence of the species lower than 2,500 feet.

27. *Nectarinia olivacea*: An evergreen forest species, represented in the highlands of eastern Southern Rhodesia by *N. o. sclateri* and in southern Nyasaland on both sides of the Nyasa/Shire Rift by *N. o. alfredi*. Intermediates between *N. o. alfredi* and *N. o. lowei* have recently been obtained near Lusaka.

28. *Antheptes longuemarei*: A Brachystegia woodland species, represented in northern Mashonaland and eastern Southern Rhodesia by *A. l. nyassae*. In Northern Rhodesia and Nyasaland west of the Nyasa/Shire Rift the form is *A. l. angolensis*, but to the east *A. l. nyassae* reappears. In Northern Rhodesia *A. l. angolensis* has recently been obtained on the very lip of the Zambezi escarpment in the Choma District at 17°00' S., 27°20' E.

29. *Serinus gularis*: A Brachystegia woodland species; *S. g. gularis* in Southern Rhodesia, *S. g. reichardi* in Nyasaland and in Northern Rhodesia, where it occurs as far south as the Kalomo District (Benson, 1959). The statement by Vincent (1952) that *S. g. reichardi* occurs in the Lower Zambezi Valley cannot be accepted (Clancey, 1960).

30. *Fringillaria capensis*: *F. c. plowesi* inhabits rocky localities in Southern Rhodesia, and is replaced in Northern Rhodesia east of the Luangwa Rift and in Nyasaland and Portuguese East Africa by *F. c. vincenti*. On the Chimanimani Mts. there occurs a more distantly related form, *F. c. smithersii*. See Irwin (1958).

Although *Centropus t. grillii* is recorded for Northern Rhodesia and Nyasaland, and *C. t. wahlbergi* for Southern Rhodesia, Irwin (in MS for *Bull. Brit. Orn. Cl.*) has shown that they are synonymous, so that this species cannot be included above.

Although 30 instances are given above of the subspecific differences between the two sides of the Zambezi Valley (contrarily in some cases the same subspecies as in Southern Rhodesia occurs in part of the area to the north), it is particularly noteworthy that there is no less a number of instances of no such differentiation anywhere on either side, even though there is no evidence at all of any gene-flow. They may be briefly mentioned by rough, somewhat arbitrary ecological categories, giving subspecific names for those (the great majority) in which trinomials can be supported:—

Brachystegia woodland: *Muscicapa adusta subadusta*, *Parus griseiventris*, *Salpornis spilonota salvadorii*, *Emberiza cabanisi orientalis* (synonym *E. c. cognominata*).

Evergreen forest: *Accipiter r. rufiventris*, *Columba a. arquatrix*, *Aplopelia l. larvata*, *Bycanistes brevis*, *Turdus g. gurneyi*, *Phylloscopus ruficapilla johnstoni*, *Malacothraupis nigrifrons sandgroundi* (see Moreau & Southern 1958), *Hypargos n. nitidulus*, *Cryptospiza reichenovii australis* (southern specimens rather larger, Smithers *et al.*, 1959).

Largely forest edges, secondary bracken growth & c.: *Cossypha caffra iolaema*, *Chloropeta n. natalensis*, *Cisticola cantans munzneri*, *Nectarinia kilimensis arturi*, *Estrilda melanotis kilimenis*.

Montane short grasslands: *Coturnix coturnix africana*, *Sarothrura affinis antonii* (for Southern Rhodesia records for these last two, see Smithers *et al.*, 1959). *Cisticola a. ayresii* (only again in extreme north of Northern Rhodesia and Nyasaland), *Hirundo atrocaerulea*.

Wet short grasslands: *Schoenicola platyura brevirostris* (see White, 1960d), *Euplectes m. macrourus*, *Ortygospiza l. locustella*.

Dry short grasslands: *Turnix nana luciana*, *Mirafraga africana transvaalensis* (see Rand, in Mayr & Greenway, 1960).

The following must also be included:—*Bubo c. capensis*, habitat uncertain (probable in Southern Rhodesia, Smithers *et al.*, 1959); *Motacilla clara torrentium*, perennial rivers and streams; *Anthus lineiventris*, rocks.

THE LUANGWA RIFT

The Luangwa River rises in the Mafinga Mts., on the Northern Rhodesia/Nyasaland border. It falls almost immediately into a wide valley floor. The altitude near the head

of the river in the Isoka District is almost 3,000 feet, and it drops gently to below 1,000 feet at its confluence with the Zambezi, some 400 miles to the south-west. The valley is as much as 40 miles across in part of the Mpika, Lundazi and Fort Jameson Districts, where the predominant vegetation is Mopane woodland, intersected by alluvial *Acacia* growth. It is enclosed by a high escarpment wall, attaining in places an altitude of near 6,000 feet down the western side from the Mpika District southwards. There is also a steep escarpment on the eastern side in the Isoka District down to the neighbourhood of the Ruwumbu, but below this point the eastern escarpment consists merely of a zone of stony hills gradually rising towards the plateau, at a general level of between 3,000 and 4,000 feet. At about 14° 15' S., the valley practically disappears, foot-hills on both sides closing with the river. Mention should also be made of the subsidiary Lukusashi and Lunsemfwa troughs (the latter also known as the Luano Valley), more than 10 miles across in places, with vegetation akin to that in the Luangwa Valley. But not enough is known about the avifauna in their immediate vicinity for it to be possible to decide whether they act as barriers in any way, and so they are not dealt with below. Probably, like the Sabi, their influence is insignificant.

The annual rainfall in the Rift as a whole is less than in the surrounding plateau country, averaging 24 to 32 inches, compared to 32 to 40 inches (see map in Brelsford, 1960). By contrast to the Mopane woodland of the Rift itself, the predominant vegetation of the plateau country is *Brachystegia* woodland. The foregoing brief description is taken from Trapnell (1953), and the map in Trapnell *et al.* (1948).

In the Rift itself various birds are widespread which are unknown in the surrounding plateau country. Examples are *Pterocles bicinctus*, *Tockus erythrorhynchus*, *Lamprolornis mevesii* and *Plocepasser mahali*. The instances which follow of the Rift acting as a distributional barrier are derived mainly from Benson & White (1957) and from Benson (1953). Where additional information is available, the authority is quoted. In none of these instances does there seem to be any ecological reason why a species should not be present on both sides of the Rift, except in the case of a species-pair, such as *Macronyx fulleborni* and *M. croceus*, whose ecological requirements are very similar, and therefore replace each other. It is true that in the north of Northern Rhodesia there are forests with a damp, peaty floor, locally known as "mushitu" (Benson & White, 1957: XIII), such as are not found to the east of the Rift. But all the evergreen forest dwelling species included below in list A (1) can also exist in riparian evergreen forest, of which there is no lack to the east of the Rift.

Certain essentially montane species, found to the east of the rift in such localities as Dedza, and the Vipya and the Nyika plateaux, in Nyasaland, rising to 7,000 feet or even higher, are not included in the lists of examples below. It is true that some of them reappear in western Angola (Heinrich, 1958: Hall, 1960), but they are unknown in the highlands in the Serenje and Mpika Districts on the west of the Rift, presumably because these do not rise high enough. Examples of such reappearances are *Apaloderma (Heterotrogon) vittata*, *Melaenornis chocolatina* (= *Dioptrornis chocolatina brunnea*), *Turdus gurneyi*, *Bradypterus barratti* (= *B. mariae*), *Cisticola lais*, *Nectarinia kilimensis* and *Cryptospiza reichenovii*.

In the examples below, the number of species restricted to the western side of the Rift (list A (1)) greatly exceeds that of those restricted to the eastern side (list A (2)). All in the former category extend across from western Angola, and it is also noteworthy that in the majority of cases this is even without any subspecific variation. It is only in the case of examples 7, 9, 12, 13, 14, 16 and 19 that there is such a difference. Another striking point is that although the predominant vegetation in this extensive area is *Brachystegia* woodland, only two (examples 10 and 17) are associated with this habitat. The explanation of this may be that it is easier for such species to gain access to the opposite side of the Rift, around the northern end, or even through the Mopane woodland in the Rift itself (thus Benson & White, 1957, give odd records of such typically *Brachystegia* species as *Caprimulgus pectoralis*, and

Salpornis spilonota from the Luangwa, outside their normal habitat). There are many rather strictly *Brachystegia*-frequenting species common to the two sides of the Rift, but unknown within it. To list them would occupy an undue amount of space, but perusal of Benson & White (1957) shows the number to be approximately thirty.

In the following list, it should be noted that Musense is at the top of the western escarpment of the Rift, in the Serenje District, and at 13° 15' S., 31° 05' E. (not 30° 05' E., as given by Benson *et al.*, 1961). Any specimens mentioned as recently collected are in the National Museum, Bulawayo.

A. SPECIES WHOSE RANGE IS LARGELY OR COMPLETELY RESTRICTED BY THE RIFT.

(1) *Occurring entirely (or almost so) only on the western side, typically ranging through the north of Northern Rhodesia and the southern Congo from western Angola*

1. *Centropus cupreicaudus*: A swamp-dweller, only certainly known further east at the mouth of the Songwe River, at the north end of Lake Nyasa. Admittedly there is an old specimen from South Angoniland (the present Ncheu and Dedza Districts of Nyasaland), but as this record has not since been corroborated the specimen may well have been mislabelled. There is no geographical variation except that the Songwe birds are rather small (Traylor, 1960—it is considered that *C. c. songweensis* is a form of *C. cupreicaudus*, and that this is not conspecific with *C. monachus*).

2. *Musophaga rossae*: This monotypic species approaches the western escarpment at about 14° 30' northwards. It is unknown in Nyasaland, and at the north end of the Rift is only known as far east as Old Fife. It inhabits evergreen forest.

3. *Lybius minor*: *L. m. maccluniei* extends from western Angola eastwards, reaching the escarpment at 14° northwards. It does extend around the north end of the Rift, but only into the Karonga District of Nyasaland. Habitat as for the last species.

4. *Motacilla capensis*: *M. c. simplicissima* is widespread in Angola, and in Northern Rhodesia west of the Rift, being found in swamps as far east as Lusiwash and Shiwa Ng'andu. It is recorded by Winterbottom (1959b) from Nyasaland, but no supporting evidence for this has been traced.

5. *Turdoides leucopygia*: *T. l. hartlaubii* is widespread in Angola, and in Northern Rhodesia west of the Rift, in open grasslands with scattered low bushes.

6. *Chlorocichla flavicollis*: *C. f. flavigula* is widespread in the north of Northern Rhodesia. It reaches the western side of the Rift between Isoka and Serenje, and inhabits evergreen forest.

7. *Campephaga quiscalina*: *C. q. martini* is known from scattered localities in the north of Northern Rhodesia, in evergreen forest. It is unrecorded any further east than Kasama and the Mlembo River, in the Serenje District.

8. *Myrmecocichla nigra*: This monotypic species is widespread in Northern Rhodesia west of the Rift. Although Benson & White (1957) give its habitat as large dry plains, such as are lacking east of the Rift, it does also inhabit the edges of small dambos, which are in fact found to the east.

9. *Cossypha bocagel*: *C. b. chapini* extends across the north of Northern Rhodesia in evergreen forest, to near the western escarpment of the Rift at Danger Hill, and at Musense (Benson *et al.*, 1961).

10. *Eremomela atricollis*: This monotypic, *Brachystegia* woodland frequenting species ranges through the north of Northern Rhodesia to near the western side of the Rift at Mpika, Chinsali (Benson, 1959) and Serenje (Benson *et al.*, 1961).

11. *Cisticola brunnesens*: *C. b. cinnamomea* ranges from western Angola across the north of Northern Rhodesia, as far as the Serenje, Mpika and Chinsali District, in wet grasslands.

The same subspecies does in fact reappear on the north-east side of the Nyasa/Shire Rift, at Njombe (Lynes, 1934).

12. *Cisticola pipiens*; 13. *C. tinniens*; 14. *C. robusta*: All three species are widespread in the north of Northern Rhodesia (*C. pipiens* extending in the west south to northern Bechuanaland). The swamp-dwelling *C. p. congo* extends east to Mbesuma, thence south-west to the Mkushi River (Benson, 1959). *C. t. shiwae*, of very similar habitat, ranges east to Shiwa Ng'andu, Lusiawashi, and also the Mkushi River (Benson, 1959), while *C. r. awemba* of wet grass lands, occurs as far east as Kasama and Serenje.

15. *Dicrurus ludwigii*: *D. l. ludwigii* ranges in evergreen forest through the north of Northern Rhodesia to the Serenje and Mpika Districts. This is considered a fair example for inclusion even though the same subspecies reappears in the south of the Nyasa/Shire Rift, and in the highlands to the east thereof. There is apparently perfectly suitable habitat in the intervening area.

16. *Ploceus bicolor*: *P. b. kigomaensis* ranges in evergreen forest through the north of Northern Rhodesia to the western escarpment at Muzyabama and Danger Hill. The species is unknown further east in Northern Rhodesia, but is represented in southern Nyasaland by *P. b. stictifrons*. This case is somewhat analogous to that of *Dicrurus ludwigii*.

17. *Ploceus* (*Phormoplectes*) *angolensis*: This apparently monotypic, *Brachystegia* woodland frequenting species ranges east to the Kondolilo Falls, in the Serenje District (Benson *et al.*, 1961), and has more recently been seen by Benson at the top of the escarpment at Musense. On the east side of the Rift there occurs the very differently coloured *P. olivaceiceps* (see list A (2)).

18. *Euplectes hartlaubi*: *E. h. hartlaubi* extends in dambos to the west of the Rift, between Broken Hill and Isoka. Another very distinct form, perhaps better regarded as a distinct species, *E. psammochromius*, occurs to the east, on the Nyika, and again at Njombe (Lynes, 1934).

19. *Ortygospiza atricollis*: Widespread in various subspecies, extending even south to the Cape Province. But in Northern Rhodesia only found on plains and dambos to the west of the Rift, though also occurring in the littoral at the north end of Lake Nyasa.

20. *Lagonosticta rufopicta*: *L. r. nitidula* ranges from northern Angola to the west side of the Rift, usually being found in small thickets.

21. *Lagonosticta caerulescens*: *L. c. perreini* extends mainly in evergreen forest to the western escarpment in the Mpika and Lundazi Districts, only extending around the north end of the Rift to Muyombe, in the east of the Isoka District. The species is unrepresented further east except by an isolated record of *L. c. incana* from Mbamba Bay, in the north-east littoral of Lake Nyasa (Meise, 1937), and is not otherwise known north of the extreme south of Nyasaland.

22. *Estrilda paludicola*: *E. p. benguellensis* is found in dambos to as far east as the Mpika and Serenje Districts west of the escarpment.

(2) Occurring practically only on the eastern side, essentially generally of an eastern distribution.

1. *Bycanistes brevis*: This species is unknown west of the Rift. To the east it occurs in several localities in highland evergreen forest in Nyasaland, where it is probably not more general through competition with *B. bucinator*.

2. *Pogoniulus* (*Viridibucco*) *leucomystax*: This monotypic species is widespread in evergreen forest in the highlands of Nyasaland west of the Nyasa/Shire Rift, but is unknown to the west of the Luangwa Rift.

3. *Pogonocichla stellata*: An evergreen forest species, mainly at higher altitudes. Common in Nyasaland west of the Nyasa/Shire Rift, and in Northern Rhodesia occurs to

the east of the Luangwa Rift on the Nyika and the Mukutu Mts., and at the top end of the Rift at Old Fife.

4. *Cisticola cantans*: This species is unknown west of the Rift. *C. c. munzueri* occurs on higher ground to the east, to as low as Fort Jameson, mainly in bracken growth.

5. *Hirundo daurica*: Included in the range of *H. d. emini* is the rocky, mountainous country between the Luangwa and Nyasa/Shire Rifts. To the west, it is unknown in apparently very suitable country in the Mpika and Serenje Districts, even though it does occur in the Abercorn District, and the Upemba National Park (Verheyen, 1953).

6. *Ploceus (Phormoplectes) olivaceiceps*: This occurs in *Brachystegia* woodland at higher levels on the east side of the Rift, in Nyasaland, extending north to nearly 11°. See also list A (1) above.

7. *Serinus citrinelloides*: *S. c. hypostictus* occurs on higher ground to the east of the Rift, typically in bracken growth on the edge of evergreen forest, and is found as low as Fort Jameson. The species is only known further west in Northern Rhodesia at Abercorn, where *S. c. frontalis* occurs.

8. *Fringillaria capensis*: *F. c. vincenti* extends north to the south of the Mzimba District, on rocky hills, but the species is unknown in similar country on the western escarpment of the Rift.

It might be thought that *Aquila verreauxi*, widespread in rocky localities in Nyasaland, and only certainly recorded from Northern Rhodesia from Nyanje, to the east of the Rift, is an example. But as it has recently been recorded by Benson (1959) from the Luano escarpment it is excluded.

B. SPECIES-PAIRS SEPARATED BY THE RIFT, OR SPECIES SHOWING SUBSPECIFIC DIFFERENCES ON THE TWO SIDES

Ploceus (Phormoplectes) angolensis and *olivaceiceps* have been dealt with above. They could conceivably have been included here, but the colour-differences are so great that this seems hardly justified.

1. *Pogoniulus bilineatus*: *P. b. mfumbiri* ranges in evergreen forest from eastern Angola across the north of Northern Rhodesia to the western escarpment of the Rift at Danger Hill. *P. b. bilineatus* has been recorded in the highlands of Nyasaland west of the Nyasa/Shire Rift from the Vipya and Nyankhowa. That it is not more general in that area may be due to competition with *P. leucomystax*.

2. *Macronyx fulleborni/croceus*: *M. f. ascensi* extends across from western Angola, and is widespread in Northern Rhodesia west of the Rift. Its range approaches very closely that of *M. croceus* at the north end, in the Isoka District, this latter species being widespread in Nyasaland, and in Northern Rhodesia on the east of the Rift. They both inhabit moist, spongy grasslands, and their ranges as a whole are largely mutually exclusive.

3. *Phyllastrephus fischeri*: *P. f. cabanisi* ranges in evergreen forest from western Angola across the north of Northern Rhodesia to the western escarpment of the Rift between Mkushi and Isoka. *P. f. placidus* occurs in certain areas of forest, from Thambani to the Masuku Mts., between the Luangwa and Nyasa/Shire Rifts.

4. *Turdus olivaceus/abyssinicus*: *T. o. stormsi* is widespread in the north of Northern Rhodesia, in evergreen forest, but is unknown east of Danger Hill, and the western escarpment of the Rift at Musense (recent sight-record by Benson). It is replaced in scattered localities at high altitudes to the east of the Rift by *T. a. nyikae* to as far south as about 11°, and by *T. a. milanjensis* at Dedza. *T. olivaceus* and *T. abyssinicus* have often been regarded as conspecific, but overlap elsewhere (Chapin, 1953).

5. *Phylloscopus ruficapilla*: The richly coloured western *P. r. laurae* and *P. r. eustacei*

were united by White (1960d) with *P. ruficapilla*. *P. r. eustacei* ranges in evergreen forest east to the escarpment of the Rift at Danger Hill, and Musense (Benson, *et al.*, 1961). *P. r. johnstoni* is found in the highlands of Nyasaland west of Lake Nyasa at Nchisi and north of about 11°.

6. *Camaroptera stierlingi*: According to Irwin (1960), *C. s. buttoni* ranges from the Mpika District south-west to Gwembe, Mankoya and Sesheke. The species inhabits *Brachystegia* woodland, and is unknown in the Luangwa. To the east thereof *C. s. buttoni* is replaced by *C. s. irwini*.

7. *Cisticola natalensis*: *C. n. katanga* is widespread west of the Rift, in open grasslands. It ranges south to Monze, while specimens from Kasusu, in the Kalomo District, are nearer *C. n. holubi* (Benson, 1959). Recent specimens from near Choma show a slight tendency towards *C. n. holubi*. *C. n. katanga* only ranges around the north end of the Rift to as far as Fort Hill, Nyasaland. It is otherwise replaced to the east by *C. n. natalensis*, and is unknown in the Luangwa itself.

8. *Malacotus nigrifrons*: *M. n. manningi* ranges through the north of Northern Rhodesia to Danger Hill. On the east of the Rift, *M. n. nigrifrons* occurs on the Nyika (see also Nyasa, Shire list).

9. *Pirenestes ostrinus/minor*: *P. o. frommi* is known from a few localities in the north of Northern Rhodesia, in evergreen forest, to as far east as the western escarpment of the Rift in the Lundazi and Mpika Districts. *P. minor* is known from scattered localities in the more humid parts of Nyasaland, in bracken growth on the edge of evergreen forest, including, to the west of the Nyasa/Shire Rift, the Vipya Plateau, and Furancungo (Vincent, 1936). A larger heavier billed form, named *P. vincenti* by Benson (1955b), probably a mere variant of *P. minor*, has been recorded from Furancungo. It serves to emphasise the close relationship of *P. minor* to *P. ostrinus*.

Anthus c. caffer is known from the Mpika District by two specimens, and *A. c. mzimbaensis* by one specimen from the Mzimba District, to the east of the Rift (Benson, 1955a). In view of the paucity of specimens, this case is not formally included above.

Anthoscopus caroli robertsi is recorded from the east of the Rift, intermediates between *A. c. rhodesiae* and *A. c. caroli* from the Mpika District to the west, and also in the Serenje District (Benson *et al.*, 1961). Actually such intermediates can be as well placed with *A. c. winterbottomi*, and a recent examination of material in the National Museum, Bulawayo shows the differences between this form and *A. c. robertsi* to be inappreciable. Consequently this case is not included above.

Also, it might be thought that an example is afforded by *Nectarinia olivacea alfredi* (on the east) and *N. o. lowei* (on the west). But recently intermediate specimens have been collected near Lusaka, where typical *N. o. lowei* would have been expected.

C. SOME MISCELLANEOUS INSTANCES, NOT FITTING INTO CATEGORIES A OR B ABOVE

1. *Cisticola galactotes*: *C. g. galactotes* (synonym *C. g. luapula* White, *in litt.*) is widespread in swamps in Northern Rhodesia west of the Rift. The species is unknown in the Rift itself, where there is little or no suitable habitat, but this does not explain its absence also from plateau country to the east. It occurs throughout the Nyasa/Shire Rift (*C. g. suahelica*).

2. *Cisticola chiniana*: *C. c. fortis* ranges from western Angola through the north of Northern Rhodesia, in secondary Acacia and *Brachystegia* scrub, to the western escarpment in the Mpika and Serenje Districts. In the Rift itself it is replaced by *C. c. procera* ranging eastwards into Nyasaland (White, 1960a).

3. *Sphenoeacus (Melocichla) mentalis*: West of the Rift, in rank grass growth near streams, there occurs *S. m. mentalis*, ranging east from western Angola. In the Rift itself north of about 13° 15', there occurs the paler *S. m. luangwae*, extending east to Fort Jameson (corrobo-

rated by several recent specimens). *S. m. orientalis* probably ranges throughout Nyasaland. For nomenclature as above, see White (1960d).

4. *Euplectes axillaris*: *E. a. bocagei* extends from western Angola to swamps west of the Rift, in the Northern Province. The species reappears in the Nyasa/Shire Rift, *E. a. axillaris* in the south, probably nearer *E. a. phoeniceus* in the north. This example resembles that of *Cisticola galactotes*.

Benson & White (1957) indicate that the Muchinga (the western) escarpment to the Rift is the dividing line between *Numida meleagris marungensis* and *N. m. mitrata*. But specimens recently collected at Musense, at the top of the escarpment, are intermediate. Furthermore, they record *N. m. mitrata* from Mbesuma, and Benson (1959) likewise from Isoka, both localities being to the west.

THE NYASA/SHIRE RIFT

The Nyasa/Shire Rift extends through the length of Nyasaland from north to south. The floor of the Nyasa Rift is in part occupied by the Lake Nyasa, at 1,550 feet, but in places over 2,200 feet deep, so that parts of the floor are more than 700 feet below sea-level. The Shire Rift is traversed by the Shire River, forming an intermittent outlet from Lake Nyasa to the lower Zambezi, almost at sea-level. The greater part of the Rift is bounded on either side by plateau country mainly between 3,000 and 4,000 feet in altitude, in which the predominant vegetation is *Brachystegia* woodland. This plateau country is surmounted by a number of small plateaux, attaining elevations usually of 6,000 to 7,000 feet, but sometimes exceeding 8,000 feet. Such plateaux are characterised by undulating short grasslands and evergreen forest often not merely riparian in extent. In the Nyasa section, the Rift is as much as 60 miles across, and the lake itself in places almost as much, but in the Shire section not much over 20 miles wide in the Blantyre District, and the escarpment on both sides is more gradual than further north.

In the Rift itself the rainfall average is generally higher than in the Luangwa Rift (see rainfall map in Brelsford, 1960), and the figures are only comparable from the south end of Lake Nyasa southward. In the Kotakota and Chinteché Districts, and at the north end of the lake, the annual average is everywhere at least 56 inches. In contrast to the Luangwa, too, Mopane woodland is by no means so prevalent, and in the lake littoral is unknown north of Ntakataka, in the Dedza District Acacia and palm growth (Benson, 1953: 6) is more in evidence, while from Salima northwards *Brachystegia* woodlands occur. Between Chinteché and Nkata Bay, where the annual rainfall average is as much as 80 inches, evergreen forest is even prevalent in some places. Between Nkata Bay and Livingstonia the escarpment extends for the most part directly down to the lake, and there is very little flat littoral country. By reason of the ecological conditions some species of birds which are normally only found at higher elevations extend to the level of Lake Nyasa in the Kota-kota and Chinteché Districts.

As might be expected, by contrast to the Luangwa, *Tockus erythrorhynchus*, *Lamprolornis mevesii* and *Plocepasser mahali* are by no means so generally distributed, and do not extend far north of the south end of Lake Nyasa, while *Pterocles bicinctus* is only known from the south-west of the Chikwawa District. Another rather typically semi-arid species extending to the south end of Lake Nyasa is *Amadina fasciata*.

The instances which follow of the Nyasa/Shire Rift acting as a barrier are derived so far as Nyasaland is concerned from Benson (1953). For northern Portuguese East Africa, Vincent (1933-6) has been more especially useful, while Chiperoni records are by Benson (1950). As with the Luangwa, the number of species confined to the west side of the Rift considerably exceeds those confined to the east side.

Two complications should be mentioned. See Dixey (1931), west of Fort Johnston there is high ground culminating in the peak of Piri-longwe, at a height of over 5,000 feet,

while further west the altitude drops to below 2,000 feet before rising again. From the lists below, the presence of *Sylvietta ruficapilla* and *Cisticola aberrans nyika* suggests a western affinity, but that of *Anthreptes longuemarei nyassae* an eastern. Also, west of the Shire River at Port Herald there is isolated high ground rising to over 3,000 feet (Malawi Hill). But the presence of *Buccanodon leucotis*, *Phyllastrephus flavostriatus vincenti*, *Coracina caesia* and *Camaroptera s. stierlingi* suggests eastern rather than western affinities. On the other hand, the presence of *B. molitor* suggests the latter.

A. SPECIES WHOSE RANGE IS ALMOST COMPLETELY RESTRICTED BY THE RIFT

(1) Occurring mainly on the western side

1. *Lybius leucomelas* (= *Tricholaema diadematum*): *L. l. frontatus* ranges south to Kasungu, and to Chadiza, in the Fort Jameson District (Benson, 1958), in *Brachystegia* woodland. It is unknown east of the Rift.

2. *Anthus leucophrys*; 3. *Anthus vaalensis*: Neither species is known to the east of the Rift, and the only record from within the Rift is of *A. leucophrys* from near the mouth of the River Songwe, at the north end of Lake Nyasa. To the west, *A. leucophrys* extends as far south as the River Bua, *A. vaalensis* to Ncheu.

4. *Parisoma lugens*: On the west, extends south to 15° 30', but on the east unknown south of the Matengo Highlands (Sassi & Zimmer, 1941). This species is largely confined to trees of *Acacia abyssinica* (= *A. woodii* in Benson, 1953), of which there is no lack in southern Nyasaland to the east of the Rift.

5. *Melaenornis (Dioptornis) chocolatina*: On the west, on the edge of montane evergreen forest to as far south as Dedza, but on the east unknown south of Njombe (Lynes, 1934).

6. *Muscicapa (Myopornis) boehmi*: Ranges in *Brachystegia* woodland on the west side south to Kapiriuta. Unknown to the east, though known on the east side of Lake Tanganyika as far north as Tabora.

7. *Elminia albicauda* (= *Erannornis longicauda*): On the west south in *Brachystegia* woodland and the edge of riparian forest to Zobue, but on the east unknown south of the Matengo Highlands (Sassi & Zimmer, 1941).

8. *Turdus litsipsirupa*: On the west, south in *Brachystegia* woodland to Ncheu; on the east known only from Njombe (Sassi & Zimmer, 1941).

9. *Erythropygia barbata*: Ranges south, mostly in *Brachystegia* woodland, to the River Bua and Fort Jameson, on the western side. In the Rift itself, occurs in this type of habitat near Kota-kota and Karonga. Only the closely related *E. quadrivirgata* occurs to the east of the Rift (and in the Rift itself), but probably never in so open a type of habitat as *Brachystegia*.

10. *Apalis porphyrolaema* (= *A. bamendae*): Occurs on the west south to about 14° 30', in highland evergreen forest, but unknown on the east side south of Njombe (Lynes, 1934).

11. *Sylvietta ruficapilla*: General on the west, in *Brachystegia* woodland, and also known from Piri-longwe. Although it extends sparingly to the littoral of Lake Nyasa at Kota-kota and Karonga, unknown to the east of the Rift.

12. *Cisticola rufilata*: Only on the west side, in scattered secondary *Brachystegia* scrub localities from the Ncheu District to Mzimba.

13. *Hirundo dimidiata*: Only on the west side, sparsely throughout from Ncheu northwards, in clearings in *Brachystegia* woodland.

14. *Hirundo semirufa*: Recorded from the Ncheu and Dedza Districts, and from Fort Jameson, associated with moist, spongy grasslands. Probably general west of the Rift, but no records from the east.

15. *Parus griseiventris* (= *P. afer*): General in *Brachystegia* woodland on the west side, extending into south western Tanganyika, but unknown to the east of the Rift. Regarded

as a species distinct from *P. afer*, following Hall & Traylor (1959) and Irwin (1959).

16. *Parus leucomelas*: General in open country with scattered bushes on the west side, only extending around the north of Lake Nyasa to Njombe (Lynes, 1934).

17. *Nectarinia kilimensis*: Distribution as for the last species; mainly on the edges of evergreen forest, rarely below 4,500 feet.

18. *Antheptes anchietae*: On the west, extends south to Dedza, and Furancungu (Vincent, 1933). Inhabits mainly the margins of *Brachystegia* woodland. A monotypic species, ranging across from western Angola, and in Tanganyika only known from the extreme west (Moreau, 1947).

19. *Euplectes macrourus*: Extends south on the west to Dedza, in moist, spongy grasslands, only extending around the north end of Lake Nyasa to Njombe (Lynes, 1934).

Macronyx ameliae is not formally included above, since although it is unknown east of the Rift, and does occur to the west in the Ncheu, Dedza and Lilongwe Districts, its occurrence is patchy. At the north end of Lake Nyasa it occurs at the mouth of the Songwe River, and Alexander (1899) records it from Chicowa, in the Zambesi Valley west of Tete.

(2) *Occurring only on the eastern side (all forest species)*

1. *Buccanodon leucotis*: From Mlanje and Cholo to Zomba; also at Malawi. Range as a whole from Natal to Kenya.

2. *Apalis melanocephala*: In scattered localities throughout the eastern side, from Chiperoni and Mlanje to Songea, with a general range from Beira and eastern Southern Rhodesia through eastern Tanganyika to Kenya.

3. *Apalis chariessa*: From Cholo and Mlanje to Chikala, and at Chiperoni. Otherwise only known from the Uluguru Mts., Tanganyika and the Tana River in Kenya.

4. *Oriolus chlorocephalus*: From Cholo to Chikala, also at Chiperoni, and in scattered localities in eastern Tanganyika.

Coracina caesia is not formally included above, because although it is known from evergreen forest at Cholo, Chiradzulu, and Chiperoni, it also occurs west of the Shire River at Malawi (Long, 1959) and again at the extreme north end of Lake Nyasa (Bangs & Love-ridge, 1933). *Alethe choloensis* is another species difficult of formal inclusion. It is endemic to evergreen forests east of the Rift, in Nyasaland from Cholo and Mlanje to Mangoche, and as far east in Portuguese territory as Namuli. The genus is unrepresented in forests west of the Rift except by *A. fulleborni*, but ranging south only to about 11°.

B. SPECIES-PAIRS SEPARATED BY THE RIFT, OR SPECIES SHOWING SUBSPECIFIC DIFFERENCES ON THE TWO SIDES

1. *Tauraco persa*: This species, inhabiting mainly evergreen forest, is represented on the west by *T. p. schalowi*, on the east by *T. p. livingstonii*, though the latter extends around the north end of Lake Nyasa, the two forms occupying adjacent ground in the neighbourhood of the Songwe River. The Rift itself is practically entirely occupied by *T. porphyreolophus*, also found in plateau country to the west in the Mzimba and Karonga Districts, though the two species are almost entirely mutually exclusive. The foregoing is derived largely from Moreau (1958).

2. *Buccanodon whytii*: *B. w. sowerbyi* occurs in *Brachystegia* woodland west of the Rift from Dedza to the Mzimba District, being probably replaced in the Karonga District by *B. w. stresemanni*. On the east it is replaced by *B. w. whytii*, ranging north to Mangoche, and easily distinguished by the pattern of the crown and forehead. A form of evidently very similar head-pattern, *B. w. euroum*, occurs in the Songea District, also to the east of the Rift (Clancey, 1956).

3. *Pogonulius (Viridibucco) leucomystax/simplex*: These two closely related monotypic

species are almost entirely separated by the Rift. Both are largely confined to evergreen forest. On the west, *P. leucomystax* is found from about 15° S., usually above 5,000 feet, and ranges north through Tanganyika, though absent from the extreme east, to central Kenya. On the east of the Rift it is only known from Njombe (Lynes, 1934). *P. simplex* occurs in Nyasaland on the east at Mangoche and Namizimu and sparsely within the Rift, to the east of the Shire River, near Fort Johnston in thickets. It is known from Sul do Save (Pinto, 1960), and in eastern Tanganyika and coastal Kenya.

4. *Phyllastrephus flavostriatus*: An evergreen forest species represented east of the Rift in southern Nyasaland and neighbouring Portuguese territory, and at Malawi, by *P. f. vincenti*, while on the west *P. f. alfredi* occurs as far south as Nchisi.

5. *Batis molitor/soror*: According to Irwin (in ms. for Ostrich), *B. molitor* is the species to the west of the Rift, *B. soror* to the east. One or the other is widespread within the Rift, but their exact distribution requires further investigation. *B. soror* occurs at Mbamba Bay; *B. molitor* at Chinteché, and at Malawi and in surrounding lowlands only *B. molitor* occurs. Both occur in any type of open woodland.

6. *Bessonornis anomala*: This species is unaccountably absent from various localities where there is suitable habitat (evergreen forest) on the two sides of the Rift, but may perhaps be fairly included. On the east, *B. a. anomala* occurs at Mlanje, and at Chiperoni, while *B. a. grotei* occurs at Songea, and apparently intergrades around the north end of Lake Nyasa with *B. a. macleodii*, extending south on the west to the Vipya Plateau. See Moreau (1950).

7. *Apalis thoracica*: The striking feature of this case is that, associated with evergreen forest at Zomba and Mlanje, on the east of the Rift, there occurs the very richly coloured *A. t. flavigularis*, while on the west side, separated by only some fifty miles at the nearest point, there occurs the very distinct *A. t. whitei*. This case is all the more remarkable because White (1960c) regards *A. t. whitei* as a synonym of *A. t. arnoldi*, of eastern Southern Rhodesia, these two being much more widely separated from each other (by the Zambezi Valley) than is *A. t. whitei* from *A. t. flavigularis*. Further north on the west side of the Rift, on the Vipya and Nyika plateaux, there occurs *A. t. youngi*. Another anomaly may here be mentioned, in that to the west of the Luangwa Rift, in the Mpika and Serenje Districts, there occurs a population also identified by White (1960c) as *A. t. arnoldi*. Also, on the north-east side of the Rift, in the Songea District, there is a population assigned by Mackworth-Praed & Grant (1955) to *A. t. whitei*! Incidentally these authors, no doubt on account of the marked difference in intensity of pigment, place *A. t. flavigularis* in a different species from the other forms mentioned above.

8. *Camaroptera stierlingi*: According to Irwin (1960), *C. s. stierlingi* is the form to the east of the Rift, and also occurs at Malawi, while on the west it is replaced by *C. s. irwini*. The species does occur very sparingly within the Rift. Investigation is needed as to the subspecific status of such populations.

9. *Cisticola aberrans*: Following White (1960b), *C. emini* is conspecific with *C. aberrans*. *C. a. nyika* occurs throughout Nyasaland west of the Rift, usually among rocks in *Brachystegia* woodland. It is also found at Pirilongwe. East of the Rift it is replaced by *C. a. lurio*.

10. *Lanius collaris*: A case requiring further investigation and collecting, Benson (1953) gives *L. c. humeralis* for the whole of Nyasaland. But Benson & White (1957) give *L. c. capelli* for throughout Northern Rhodesia, and this may be the subspecies in Nyasaland west of the Rift, with *L. c. humeralis* confined to the east. The species occurs uncommonly as low as 1,500 feet in the Rift itself, and the subspecific status of such populations also requires investigation.

11. *Malaconotus (Chlorophoneus) olivaceus*: *M. o. makawa* inhabits evergreen forest to the west of the Rift, on the Kirk Range north to Chongoni. To the east, it is replaced by *M. o. bertrandi* at Mlanje, Zomba and Malosa.

12. *Malaconotus (Chlorophoneus) nigrifrons*: *M. n. sandgroundi* occurs in evergreen forest east of the Rift from Cholo and Mlanje to Mangoche. The species is absent west of the Rift south of the Nyika Plateau, where the subspecies is attributed by Rand (in Mayr & Greenway, 1960) to *M. n. nigrifrons*, ranging north to Kenya and around the north end of Lake Nyasa to Songea (Moreau & Southern, 1958).

13. *Anthreptes longuemarei*: *A. l. angolensis* occurs throughout west of the Rift, mainly in *Brachystegia* woodland, only extending to Lake Nyasa at Kota-kota and Karonga. East of the Rift, and at Piri-longwe, it is replaced by *A. l. nyassae*.

THE ALBERTINE RIFT

The Albertine Rift is formed by the lake chain from Lake Albert to the south end of Lake Tanganyika. Both sides of Lake Albert consist of a forest and savanna mosaic with the Lendu Plateau on the west side rising to summits over 7,000 feet. Between Lakes Albert and Edward the massif of Ruwenzori forms a high ridge on the east of the Rift, and the eastern side of the Rift forms an escarpment from east of Lake Albert to the highlands of Ruanda and Urundi. On the west from north-west of Lake Edward to the ridges west of Lake Kivu and north-west of Lake Tanganyika the edge of the Rift is more elevated rising to 10,000 feet. The southern end of this western ridge (Itombwe) with Mt. Mohi over 10,000 feet is followed by a depression formed by the Kilombwe River. South of this a further massif (Kabobo) rises to a little over 8,000 feet, and this is followed by the valley of the Lukuga River which runs into Lake Tanganyika at Albertville. Further south again is the plateau of Marungu, rising to about 6,000 feet.

South of the Urundi Highlands there are few high points on the east of Lake Tanganyika. The most important of these is the Kungwe Mahare mountains almost opposite Albertville and separated from the Urundi Highlands by the Malagarasi Valley. Further south and opposite the Marungu Highlands, there are the Ufipa Highlands on the east of the lake.

In considering the significance of the Albertine Rift discussion will be confined to passerine birds and mainly to those found in forest, montane, or lowland.

The Rift where it forms the boundary between the Congo and Uganda evidently forms no barrier for the passage of a great many forest birds which extend east in varying degrees into Uganda and western Kenya. There are however a number of cases of lowland forest birds which do not extend east of the Rift, and therefore are either unknown from Uganda or only recorded there from Bwamba on the west of Ruwenzori.

Examples are *Smithornis sharpei*, *Baeopogon clamans*, *Criniger barbatus*, *C. ndussumensis*, *Thescelocichla leucopleura*, *Chlorocichla simplex*, *Phyllastrephus icterinus*, *P. lorenzi*, *Nicator vireo*, *Turdus oberlaenderi*, *T. crossleyi* (if treated as specifically distinct from *gurneyi*), *Muscicapa olivascens*, *M. epulata*, *Pedilorchynchus tessmanni*, *Diaphorophya tonsa*, *Psaldiprocne nitens*, *Malaconotus cruentus*, *Dryoscopus sabinii*, *Nectarinia batesi*, *N. minulla*, *Ploceus albinucha*, *P. aureonucha*, *P. preussi*, *P. dorsomaculatus*, *Malimbus coronatus*, *M. nitens*, *M. erythrogaster*, *M. flavipes*, *Parmoptila woodhousei*, *Spermophaga poliogenys*, *Nigrita luteifrons*, *N. bicolor*.

In the case of the lowland forest species which do cross the Rift, however, there is practically no subspecific difference between populations of west Uganda and the west side of the Rift, a conspicuous exception being however *Anthreptes collaris*. The Rift in this area at its northern end thus presents an anomalous picture. On the one hand it has evidently proved no obstacle to the numerous lowland birds, the Uganda populations not even being sufficiently isolated to have developed subspecific variations. On the other hand about 32 lowland forest passerines have failed to cross the Rift.

Turning to montane forest species, the only montane areas on the north-east rim of the Rift in the north are provided by Ruwenzori and Kigezi. Ruwenzori is slightly anomalous, since although strictly part of the eastern side of the Rift, the Rift bifurcates slightly to its

south to take in Lake George. Unknown from the mountain forests east of the Rift in this area are *Pseudocalymptomena graueri*, *Lioptilus rufocinctus*, *Graueria vittata*, *Hemitesia neumanni*, *Cossypha roberti*, *Malaenornis ardesiaca*, *Muscicapa lendu*, *Prionops alberti*, *Nectarinia rockefelleri*. Some of these however do occur east of the Rift further south in the Rugege forest area of Ruanda, and may perhaps be found eventually in Kigezi.

Ruwenzori itself is the focus of a small amount of rather slight subspecific differentiation in its montane birds, having peculiar forms of *Phylloscopus umbroviensis*, *Nectarinia alinae*, *N. regia* and *N. afra*. The amount of subspecific variation due to any isolation of Ruwenzori is thus less than the peculiarities of absent species occurring in the adjacent Rift Valley mountains west and south.

West of the Rift in this area the main peculiarity is furnished by the isolated position of the Lendu plateau west of Lake Albert. Some montane species occurring in the main chain further south are absent there (e.g. *Graueria*, *Cossypha roberti*, *C. bocagei*, *Alethe archeri*, *Lioptilus rufocinctus*, *Parus fasciiventer* etc). One or two subspecies (e.g. *Muscicapa l. lendu*, *Sylvietta leucophrys chapini*, *Dioptrornis chocolatina demicincta*) are peculiar to the Lendu plateau. Since it occupies an isolated position at the northern extremity of the western wall of the Rift, and apparently the forest has been extensively destroyed on the Lendu plateau, it is not surprising that it should have a somewhat impoverished montane fauna, although it is perhaps poorer than might have been suspected from its position.

Further south from west of Lake Edward to Itombwe the forest fauna of the western side of the Albertine Rift exists in its most developed form. A considerable number of the species of this fauna have been able to cross the gap caused by the Kilombwe river, and reappear on Mt. Kabobo in identical or distinguishable forms. Absent south of the Kilombwe however are *Pseudocalymptomena graueri*, *Coracina graueri*, *Graueria vittata*, *Sheppardia aequatorialis*, *Cossypha roberti*, *Malaenornis ardesiaca*, *Malaconotus multicolor*, *Malaconotus lagdeni*, *Poocoptera stuhlmanni*, *Cinnyricinclus sharpii*, *Nectarinia purpureiventris*, *Ploceus insignis* and *Linurgus olivaceus*. Some other absent species are attributable to the fact that Kabobo is not high enough for them. A standard comparative list of montane species, mainly forest, is difficult to draw up since opinions will differ as to the inclusion of certain species. The list which we have used contains 64 passerine species associated with the main area of the western chain on the Congo side of the Rift. About two thirds of these occur also on both Ruwenzori and on Mt. Kabobo, so that the gap south of Itombwe is faunistically as important as the Rift west of Ruwenzori in terms of being a species barrier. If subspecific variation is also taken into account this is greater on Kabobo than on Ruwenzori, so that the Kilombwe valley appears to be a greater isolating factor than the Rift west of Ruwenzori.

The Lendu plateau is decidedly poorer than either Kabobo or Ruwenzori, apparently only possessing about half of the 64 species.

Three montane areas remain for comment. Of these Kungwe Mahare is the most important as it might be regarded as an outlier of the main Rift chain ridges on the south, mid way down Lake Tanganyika. However its montane fauna, although interesting, is very deficient in species as compared with the main western chain. Out of the standard list of 64 species, only 16 are known to occur on Kungwe. Kungwe is isolated by Lake Tanganyika from Mt. Kabobo, and judging by the great absence of species of Mt. Kabobo, the lake forms a major barrier. However the gap between the Urundi highlands and Kungwe is evidently equally a barrier. Ufipa and the Marungu highlands are even poorer. On Marungu the presence of *Apalis pulchra*, *A. binotata*, and *Nectarinia afra*—all found in the western Rift chain, but not on Ufipa—suggests that Marungu may have derived a very scanty part of its fauna from the Rift chain. Ufipa has no elements to suggest any close connection with the Rift chain, and has a fauna more closely related to other East African mountains.

The overall conclusion is that the Albertine Rift like any other ecological gap presents a barrier to the dispersal of species but its significance is less than might be supposed. The faunas of Kabobo and the Rendu plateau, though separated from the main western montane chain by less striking physical features than the Albertine Rift, show similar deficiencies in their fauna as compared with the main chain. Kungwe with the double barriers of an unsuitable land gap to the north and a water gap to the west has few of the possibly expected species, whilst the southern massifs of Marungu and Ufipa, although part of the Rift valley system are evidently too isolated to belong faunally to the montane fauna of the main chain.

In considering the poor faunas, relatively speaking, of Kungwe, Marungu and Ufipa, a further factor should be taken into account in addition to the physical isolating factors. All three have much smaller areas of forest to provide niches for species than the areas further north. In this respect they are analogous to small islands as distinguished from larger islands in insular faunas, and their reduced size must in itself be a limiting factor. Secondly they lack the altitude of the main more northern areas, another limiting factor; this however is less serious, in all probability, than size and isolation, since Kabobo is no higher but has an incomparably richer fauna.

The foregoing account of the Albertine Rift is derived largely from Chapin (1932-54); Moreau (1943), for Kungwe and Ufipa; and Prigogine (1960), for Kabobo.

THE KENYA RIFT VALLEY

The profile of west and central Kenya may be described as follows: (i) the eastern shore of Lake Victoria and the country north of it, which includes some forest areas; (ii) the high ridge of the Mau escarpment and Mt. Elgon, forming the west rim of the Rift valley; (iii) the trough of the Rift, much drier than the foregoing; (iv) the central highlands of Kenya east of the Rift. These form the east rim of the Rift. The two rims of the Rift contain considerable montane forest.

For birds extending east from Uganda where except on the Uganda rim of the Albertine Rift, forest is lowland, there are thus two obstacles. The first of altitude provided by the Mau escarpment, and the second of aridity provided by the Rift in Kenya. That one or other of these factors is an obstacle is clear, since many species found in Uganda extend east no further than west Kenya. There are however a few anomalous cases such as *Mala-cocincla rufipennis* and *Neocossyphus rufus*, which occur both in lowland East Africa and in Uganda or West Kenya, and have evidently crossed both the montane highlands and the Rift Valley.

Unlike the Albertine Rift, the Kenya Rift is not only an obstacle to the passage of certain species, but also an isolating factor which has resulted in subspeciation of a number of species which occur on either side of it. About twenty such instances occur among passerine birds, of which the following may be cited as examples.

Species	Western Form	Eastern Form
<i>Mirafrax rufocinnamomea</i>	<i>kavirondensis</i>	<i>torrida</i>
<i>Phyllastrephus fischeri</i>	<i>cabanisi</i>	<i>placidus</i>
<i>Alethe poliocephala</i>	<i>carruthersi</i>	<i>akeleyae</i>
<i>Turdus piaggiae</i>	<i>piaggiae</i>	<i>kilimensis</i>
<i>Eremomela scotops</i>	<i>citriniceps</i>	<i>kikuyuensis</i>
<i>Laniarius ferrugineus</i>	<i>major</i>	<i>ambiguus</i>
<i>Zosterops senegalensis</i>	<i>jacksoni</i>	<i>kikuyuensis</i>
<i>Nectarinia olivacea</i>	<i>vincenti</i>	<i>neglecta</i>
<i>Ploceus ocularis</i>	<i>crocatus</i>	<i>suahelicus</i>
<i>Serinus burtoni</i>	<i>gurneti</i>	<i>albifrons</i>

The genus *Platysteira* presents an interesting example of two species forming a super-species in which not the Rift, but apparently competition provides the isolating factor, since *P. peltata* occurs on both sides of the Rift, but only in the escarpment in the west, being replaced at lower levels by *cyanea*. *Turdus piaggiae* and *gurneyi*, a closely related species-pair are somewhat analogous, since *gurneyi* does not cross to the west of the Rift in Kenya, whilst *piaggiae* does cross to the east as far as the central highlands of Kenya.

Considering how pronounced a physical feature the Kenya Rift valley is, its effect in permitting subspeciation between populations of the same species on either side of it are not very striking, although its effect as a total barrier to species dispersal is obvious. However we have seen that the Albertine Rift, a less extreme barrier has an equally marked effect. In addition any obstacle to continuous distribution is likely to affect species dispersal, as shown by the isolation of such localities as the Lendu plateau and Mt. Kabobo in relation to the main chain of the western rim of the Albertine Rift. This would suggest that Rift valleys are merely one of the various ways in which populations may be isolated by the existence of an unsuitable environment between them. The Kenya Rift, because it presents such an obvious barrier, might be expected to have had a more pronounced effect than in fact seems to be the case, since equally marked effects can be associated with less spectacular barriers. Overall then, the significance of an apparent barrier depends less on the extreme nature of the contrasting environment than on the ability or inability to cross it. Thus *Laniarius* forms and *Phyllastrephus* forms cited above do in fact intergrade, showing that gene flow is not completely prevented by the existence of the Rift. The water barrier of Lake Tanganyika seems to be a more effective barrier to movement between Kabobo and Kungwe than the unfavourable land barrier of the Kenya Rift.

The foregoing account of the Kenya Rift is derived largely from Jackson & Selater (1938).

GENERAL DISCUSSION AND CONCLUSIONS

Apart from the isolating factors which, as mentioned in the introduction, affect distribution of species and give rise to discontinuous populations as a result of rift and river valley conditions, the following points merit mention:—

(1) Considering *Brachystegia* woodland, it is particularly noteworthy that out of the Luangwa list of 22 species largely confined to the west of that Rift, only two are associated with this habitat. It is relatively easy for them to extend further west, around the northern end. There are however a further 10 species largely confined to the west of the Nyasa/Shire Rift (see list A (1) thereunder, Nos. 1, 6, 7, 8, 9, 11, 12, 13, 15, 18). By contrast, there is not a single *Brachystegia* species confined to the east of these two Rifts, if *Ploceus olivaceiceps* is excluded, probably ecologically analogous to *P. angloensis*. Possibly the main centre of evolution of such species has been west of the Luangwa Rift. All of those mentioned range to western Angola. It is also noteworthy that there are eleven species listed from north of the Zambezi but unknown in Southern Rhodesia (one of them occurs in the Sul do Save). By contrast, there is not a single one occurring in Southern Rhodesia which does not reappear north of the Zambezi. *Brachystegia* is unknown south of the Limpopo, with the result that the Zambezi list A (1) contains 15 species associated with this habitat. Subspeciation concerns nine *Brachystegia* woodland species (considering the Zambezi, Luangwa and Nyasa/Shire lists as a whole).

(2) Turning to the other most important habitat (evergreen forest, including edges), only four species do not range north of the Limpopo. Of these, this only applies really strictly to *Cossypha dichroa*, the other three (*Mesopicos*, *Liopitilus* and *Serinus scotops*) all being represented north of the Zambezi. On the other hand there are seven species not extending south of the highlands of eastern Southern Rhodesia, two of which (*Pogonochila swymertoni* and *Prinia robertsi*) are endemics, and a third (*Apalis melanocephala chirindensis*) at least a well

marked endemic subspecies. The number of species confined to the north of the Zambezi is 15, and could be increased very considerably if species occurring in northern Nyasaland and the north of Northern Rhodesia (for which of course there is no evidence that the Zambezi Valley is acting as a barrier) were added. According to Moreau (1952: 594) only 16 out of the 116 African montane forest passerine species occur south of the Zambezi. By contrast to *Brachystegia* woodland, there are 10 species (including *Coracina caesia* and *Alethe* spp.) not extending west of the Luangwa Rift or even the Nyasa/Shire Rift (see the respective lists A (2)). Thus speciation in this eastern area may have been more active in the case of evergreen forest than *Brachystegia* species. Subspeciation is much more marked than in the case of *Brachystegia*, and concerns 20 species. There are however some curious anomalies in both ecological categories, as already mentioned. Thus one must postulate a recent connection (evergreen forest in a colder regime—presumably via the humid littoral of Portuguese East Africa) to explain the existence of identical populations of *Andropadus milanensis* in eastern Southern Rhodesia and north of the Zambezi at Mlanje, Chiperoni and Namuli (see Zambezi list B). Furthermore, at the end of the Zambezi list there is a long list of species in various ecological categories for which there is neither any present evidence of any gene flow nor of subspeciation. In this connection the reader is referred to Zeuner (1950, 1959), for a discussion of climatic oscillations.

(3) Attention should be drawn to the case of several species found south of the Limpopo and absent from Southern Rhodesia, yet reappearing north of the Zambezi. It has already been suggested in the case of *Mesopicos griseocephalus* that this might be due to competition with *Campethera abingoni*. Again, in the case of *Anthus leucophrys*, *A. vaalensis* or *A. novae-seelandiae* might be the competitor, and in the case of *Cisticola textrix*, *C. aridula*, as already suggested by Benson and White (1961). *Serinus scotops*, apparently closely related to *S. citrinelloides*, presents a different problem, as there is no analogue in Southern Rhodesia. In the Zambezi list A (1), there are the cases of *Columba guinea* and *Eurocephalus anguimitens* unknown in Northern Rhodesia and Nyasaland, but reappearing in the Rukwa Valley. They both seem to have a preference for semi-arid country and the appropriate conditions for their occurrence apparently do not at present exist in this intervening area.

(4) Formally included in the Limpopo, Zambezi, Luangwa and Nyasa/Shire lists are only 20 non-passerine species compared to 127 passerines. The highest totals for the latter are Sylviidae (30) and Turidae (18). Even the Hirundinidae (four) are represented.

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DISCUSSION

- Mr. Liversidge*: Chapin suggests that the savannah fauna is derived from a forest fauna, and I have been struck by the absence of endemic species in the arid regions of South West Africa.
- Mr. Stuart Irwin*: I do not believe that the forests of Africa were very much greater in the past than they are today, and think that much was always covered by savannah.
- Dr. Stuckenberg*: There is evidence of a considerable increase in the Congo forests in the past 12000 years and parts are believed to be of very recent origin.
- Dr. Winterbottom*: While I would not dispute that *Brachystegia* has many forms peculiar to it, I think the authors tend to overemphasize this and so obscure the fact that it also has many species in common with other types of woodland, some of these extending well down into the Transvaal.
- Mr. Stuart Irwin*: I agree that there are many species which one cannot use in trying to determine the past significance of physical barriers.
- Dr. Winterbottom*: If there are so many species which cannot be used, it seems doubtful whether the distinction is real or important.

Prof. Ewer: There is again confusion between the "lumpers" and the "splitters". Irwin has shown how a study of species which respect barriers can reveal something of the history of the fauna; but wide-ranging species do not show anything comprehensible.

Mr. Atwell: Is there any case of a river acting as a barrier to avian dispersal in the areas considered?

Mr. Stuart Irwin: While no positive instance is known, *Francolinus hildebrandti* occurs on the north side of the Zambezi and *F. natalensis* on the south side at Tambara. It has been suggested that the birds are conspecific and the river may be a barrier between the two forms which are probably very sedentary. In the Balovale district the two sides of the Zambezi show marked contrasts in avifauna which must, however, be attributed to equally marked differences in the environment, as *Brachystegia* woodland predominates in the east and open plains in the west. Lake Mwera-Wa-Ntipa may also act as a barrier in certain respects, probably through lack of the correct ecological conditions for certain forms.

Prof. van Zinderen Bakker: In considering this problem, one must remember that conditions were generally hotter and more arid during the Tertiary. Botanically, the Moçambique plain does not conform well to the pattern of *Brachystegia* woodland elsewhere.

Mr. Stuart Irwin: The same applies to the avifauna, and temperature appears to be a limiting factor, since the highland forms do not generally come down into the *Brachystegia* woodlands of the plain.

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PIETERMARITZBURG.

The distribution of the
montane palaeogenic element
in the South African
invertebrate fauna

INTRODUCTION

The palaeogenic invertebrates are among the most archaic animals in our fauna, and they contribute greatly to its temperate facies. Their antiquity is revealed by a discontinuous distribution in more than one zoogeographical region, and by their confinement, within the Ethiopian Region, to South Africa. These elements are mostly relict, primitive types belonging to ancient groups usually undergoing regional evolution along distinctive lines. Their concentration in South Africa is a well-known feature, especially since it is part of a clearly-defined pattern in the southern hemisphere, which shows a stock of ancient invertebrates and plants zoned in the southern parts of the continents. The purpose of this paper is to outline the distribution of certain of the best known or most characteristic of the South African palaeogenic invertebrate groups, and to attempt some generalizations concerning the distribution of this faunal component.

The distribution of a number of these palaeogenic elements is related to a certain range of temperature and humidity conditions peculiar to montane areas, and it is some of these elements that will be considered here. Included are silvicolous groups, groups with aquatic immature stages in montane streams, and groups with terrestrial immature stages occurring in alpine grassland or macchia. The distribution of the deserticolous palaeogenic elements is quite different and must be the subject of a separate study.

Many invertebrate groups are still poorly known and badly collected, and all too frequently have not been reviewed or monographed. Hence this study is inadequately documented. Also, it is absolutely certain that data concerning examples used in this paper will have to be modified to accord with the results of future collecting, as our knowledge of most of these groups is very superficial. Indeed some of the distribution maps presented below show possibly better the spheres of activity and dispersal of staff during field trips from the South African and Natal Museums! These deficiencies are inevitable at this stage in the exploration of our fauna, and it is considered that they do not invalidate the general conclusions drawn below. Further examples of distribution patterns in palaeogenic groups can be abstracted from papers listed in the references: it will be seen that they agree in large measure with the patterns mapped in Figs. 1-7.

DISTRIBUTION PATTERNS OF SOME PALAEOGENIC GROUPS

The distribution of these invertebrates has been plotted by means of a $\frac{1}{4}^{\circ}$ square grid system on outline plotting maps supplied by the Government Printer, Pretoria.

In Fig. 1 the Limpopo and Great Fish Rivers are indicated by dotted lines, the Great Escarpment in the eastern part of South Africa by a heavy broken line, and the northern limit of the geological province of the Cape Fold Mountains by a continuous heavy line. This map shows the distribution of blepharocerid flies. There is one genus in South Africa, *Elporia* Edwards, evolved from a generalized Paltostomine and related to Palaearctic and Neotropical genera. The immature stages are torrent-dwellers, living in clear, well-oxygenated mountain streams, and this makes them eminently suitable for zoogeographical studies. The family is an old and rather isolated one. In the map the localities on the Cape Fold Ranges are distinguished by hollow squares from those of the Eastern Highlands, namely Basutoland, the entire Drakensberg Escarpment, the Amatola Range and the Eastern Plateau Slopes (for an explanation of this term see Wellington, 1946). *Elporia* extends from the Cape Peninsula to the northern end of the Eastern Transvaal Escarpment. Its species fall clearly into two assemblages, one on the Fold Mountains and the other in the Eastern Highlands, no species crossing the Fish River Valley. The Cape species are most numerous in the south-west, and there is one outlying species (related to a Cape species) on the Kamiesberg which is not a part of the Fold System (Barnard, 1947). The species of the Eastern Highlands fall into three groups (Stuckenberg, 1955, 1961b): (a) those of the Basutoland-Drakensberg Highlands, with outlying populations or related species on scarps in the Natal Midlands, Zululand and Griqualand East, six endemic species in all; (b) two species on the Amatola Range, having affinities with those of the Basutoland-Drakensberg Highlands; (c) those of the Transvaal Escarpment, and the Plateau Slopes around Barberton, four endemic species derived from the Basutoland Drakensberg Highlands. One species is common to a and c.

Fig. 2 shows the distribution of the Lucanid genus *Colophon* Gray (based on Brinck, 1956). This genus is endemic to the ranges of the south west Cape, where it has undergone intensive speciation (Barnard, 1929). Its twelve species are all apterous summit-dwellers of unusually restricted distribution, and the immature stages live in soil. *Colophon* is placed in the subfamily Lampriminae which includes otherwise only genera from South America and Australia, as well as one in Baltic amber of lower Oligocene age (see Brinck, *op. cit.*).

Fig. 3 indicates the known distribution of three genera of Diptera. *Pachybates* Bezzi (a) and *Trichacantha* Stuckenberg (b) are the only endemic genera of Rhagionidae in the Ethiopian Region (Stuckenberg, 1960a). They are related and possess a curious combination of primitive and specialized anatomical features. Their nearest relative seems to be *Atherix* Meigen, a genus with a wide range in the northern hemisphere and occurring also in South Africa as a palaeogenic element. The larvae of *Pachybates* and *Trichacantha* are aquatic, living in clear mountain streams. *Pachybates* is known only from the south-west Cape, *Trichacantha* from the forested belt between Knysna and Port Elizabeth, but it is certain that they have a wider range over the Fold Mountains than is indicated. *Peringyomyia* Alexander (c) is the only African member of the primitive family Tanyderidae. The single species, *P. barnardi* Alexander, is known from a few localities in the south-west Cape; it occurs near montane streams in the sandy margins of which its larvae live (Wood, 1952). Its affinities are uncertain, though Wood (*op. cit.*) observes that the immature stages are very like those of the Nearctic *Protoplasia* O.-S.

Fig. 4 indicates the distribution of the Megaloptera, an ancient order which in Africa is entirely confined south of the Limpopo. All its members are aquatic in the immature stages, preferring mountain streams. There are four endemic genera in two families (Barnard, 1931, 140). Corydalidae are represented by the monotypic *Chloroniella* E.-P. (a) confined

to a small area within the South-West Cape; *Platychauliodes* E.-P. (b) has five described species distributed on the mountains of the south-west Cape and in the Knysna area; *Taeniochauliodes* E.-P. (e) has a single species with a wide range, known from many localities in the south-west Cape and distributed along the Fold Mountains as far east as Storms River—it occurs also in Natal on the Drakensberg and on the outlying Karkloof Range

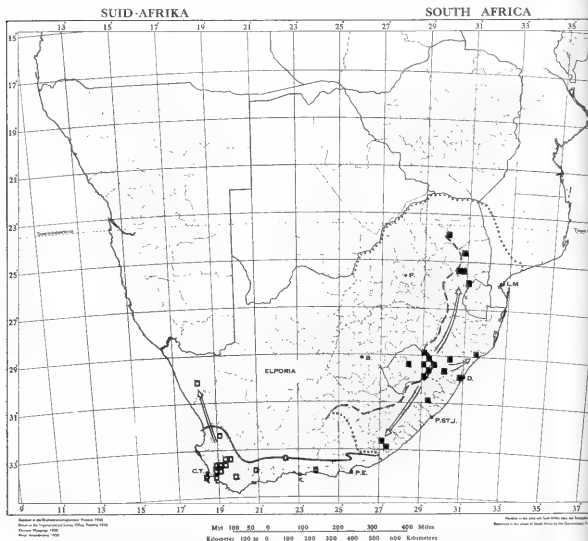


Fig. 1: The distribution of Blepharoceridae (Diptera). There is one genus, *Elporia* Edwards. Localities in the Cape Centre are indicated by hollow squares. The dotted lines trace the courses of the Limpopo and Great Fish Rivers, the continuous heavy line marks the northern limit of the Cape Fold Belt and the broken heavy line the approximate position of the eastern part of the Great Escarpment. There are three foci of speciation in the Eastern Highlands Centre.

DISTRIBUTION OF MONTANE PALAEOGENIC ELEMENT IN SOUTH AFRICAN INVERTEBRATE FAUNA

(Crass, 1949). The family Sialidae is represented by *Leptosialis* E.-P., whose single species, *africana* E.-P. (c) occurs in the south-west Cape, in the eastern Cape in the Kokstad-Franklin districts and Amatola Range, and in Natal on the Escarpment (Barnard, *op. cit.*; Crass *op. cit.*).

Fig. 5 shows the known distribution of four genera that have related forms in South America or Australasia, or both. The single South African species of the Dermapteran genus *Esphalmemus* Burr, *E. peringueyi* (Bormans), is known from the localities marked g (Hincks, 1957, 57-58). It is strictly montane and has been found in the Basutoland highlands, southern

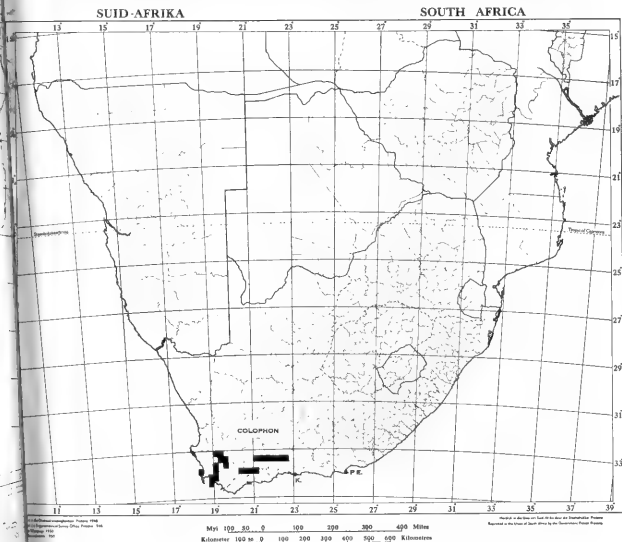


Fig. 2: The distribution of *Colophon* Gray (Coleoptera: Lucanidae).

Drakensberg, and in the Cape Fold Mountains westward to the Cape Peninsula. The only other members of the genus are five species in temperate South America. *Afrothaumalea* Stuckenberg (c), a monotypic genus of Nematocerous Diptera described only in 1960, is related to *Austrothaumalea* Tonnoir of temperate South America and Australasia. At present it is known from a female specimen found on the crest of the Natal Drakensberg and a male from the south-west Cape (Stuckenberg 1960b, 1961a). The immature stages of Thaumaleidae are known to live in seepage or thin films of water. *Atherimorpha* White (e) is an interesting

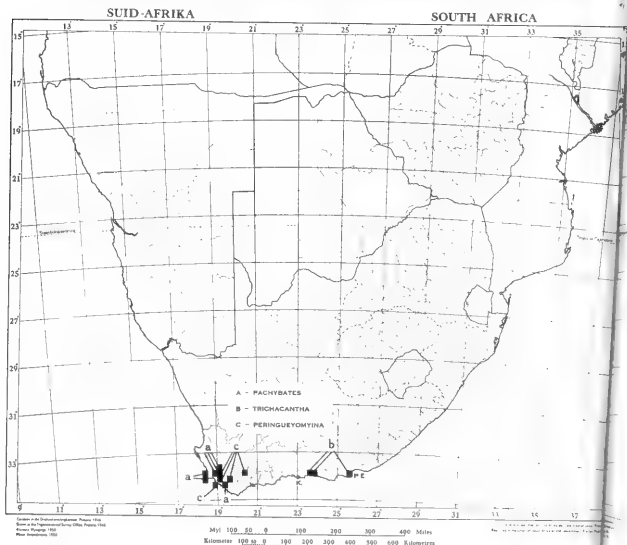


Fig. 3: The occurrence of three genera of Diptera, the Rhagionids *Pachybates* Bezzi (a) and *Trichacantha* Stuckenberg (b), and the Tanyderid *Peringueyomyia* Alexander (c).

DISTRIBUTION OF MONTANE PALAEOGENIC ELEMENT IN SOUTH AFRICAN INVERTEBRATE FAUNA

genus of Diptera with a number of South African species (Stuckenberg 1956a, 1961b); they are poorly known, being seldom collected. At least two species occur in the Basutoland-Drakensberg Highlands, an undescribed species has recently been found on the Zuurberg, and two species are on the ranges of the south-west Cape. The genus otherwise inhabits south-east Australia, Tasmania and temperate South America. In some respects the South African species show affinities with the genotype from Tasmania. *Arthrotes Bezzi* (a) is an endemic genus locally derived from *Atherimorpha*. It is strictly montane, with a species in

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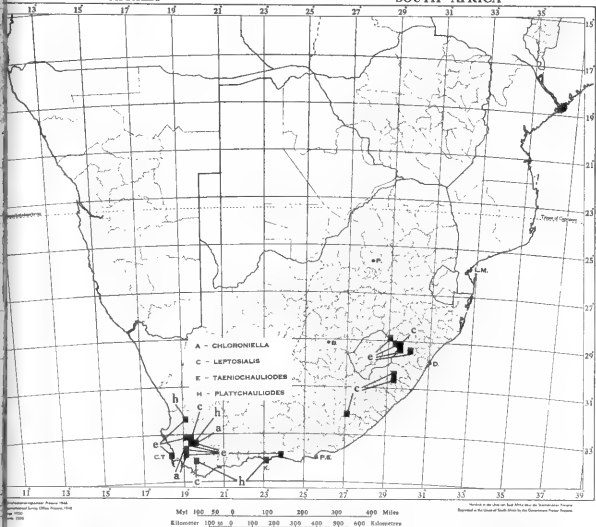


Fig. 4: The distribution of Megaloptera. The Corydalidae are represented by *Chloroniella* E.-P. (a), *Platychoauliodes* E.-P. (b) and *Taeniochauliodes* E.-P. (e); there is one genus of Sialidae, *Leptosialis* E.-P. (c).

the Natal Drakensberg and two, possibly three, in the south-west Cape (Stuckenberg, 1956b). The immature stages of *Arthroteles* and *Atherimorpha* are unknown. Both genera seem to have a preference for macchia vegetation, especially in the Cape, and possibly have terrestrial larvae.

Fig. 6 shows the distribution of the South African Onychophora, *Opisthopatus* Purcell and *Peripatopsis* Pocock (based on Brinck, 1957, and augmented by data supplied by Dr. R. F. Lawrence). On the map the Cape and the Eastern Highlands species are distinguished.

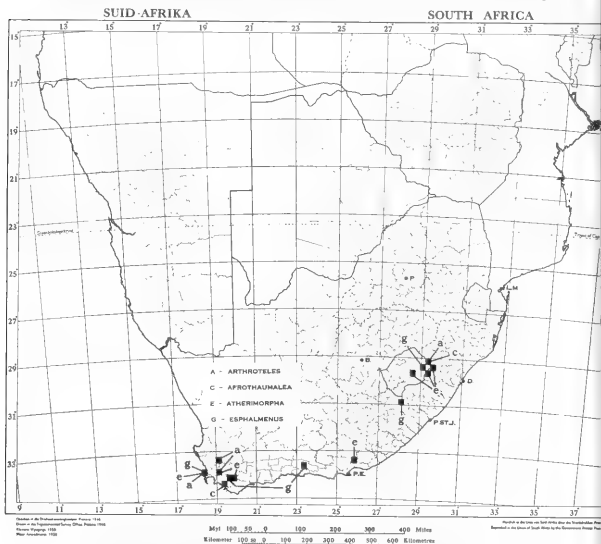


Fig. 5: The distribution of *Esphalmenus* Burr (Dermoptera); and three genera of Diptera, (c) *Afrothaumalea* Stuckenberg (Thaumaleidae), (e) *Atherimorpha* White (Erinnidae) and (a) *Arthroteles* Bezzi (Erinnidae).

DISTRIBUTION OF MONTANE PALAEOGENIC ELEMENT IN SOUTH AFRICAN INVERTEBRATE FAUNA

The genus *Peripatopsis* has its centre of distribution in the Cape Fold Mountains where there are nine endemic species; one species, *P. moseleyi* (Wood-Mason) extends from the eastern Cape to Natal, occurs in forests of the Natal Midlands and on the Amatola Range, and crosses the Fish River Valley to only the eastern end of the Fold Belt. *Opisthopatus* is an eastern genus with two species; *roseus* Lawrence seems very restricted, being known only from the highlands in the Harding District, but *cinctipes* Purcell has the widest range of all, occurring in forest on the Transvaal Drakensberg, at numerous localities in Natal, Zululand and Pondo-

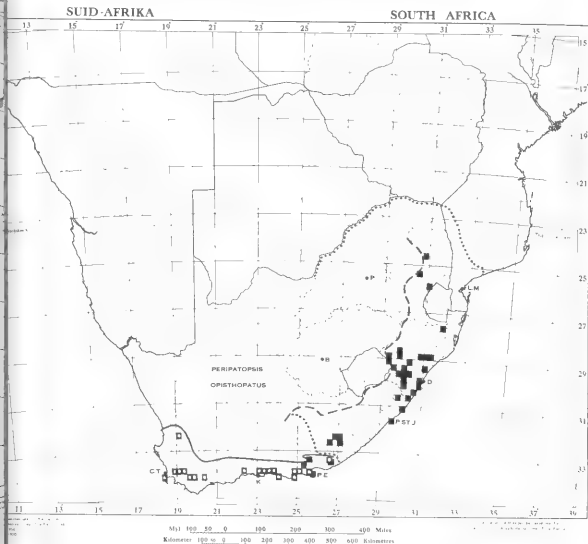


Fig. 6: The distribution of Onychophora. There are two genera, *Opisthopatus* Purcell and *Peripatopsis* Pocock. Hollow squares indicate localities for species endemic to the Cape Fold Mountains.

land, from sea-level to the upper limit of montane forest at about 5,000 ft., and like *moseleyi* also at the eastern end of the Fold Belt. In many respects the distribution of *cinctipes* is a typical of the faunal constituent being examined here, since this species is ecologically much more tolerant, living near sea-level and in places under subtropical conditions. In view of this it is surprising that it has not crossed the Limpopo Valley. The affinities of the

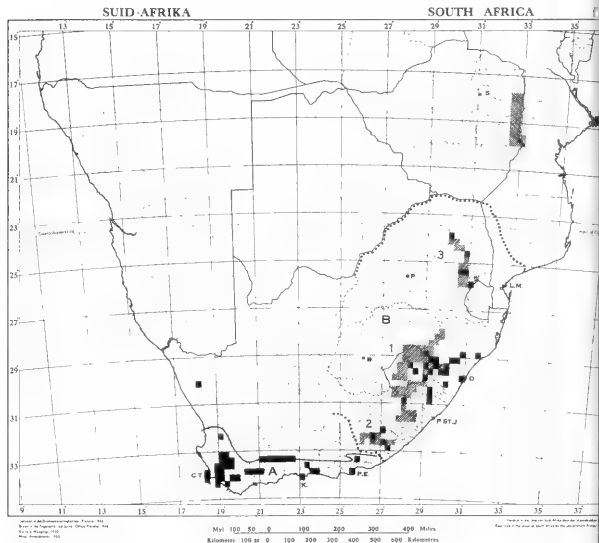


Fig. 7: This map shows all the distribution patterns in the preceding figures in combination, the records for *Opisthopatus cinctipes* being omitted (see text). Regions that probably are suitable for montane palaeogenic elements are indicated by hatching. The Eastern Highlands of Rhodesia are also hatched. Other details are as in Fig. 1.

South African Onychophora are latitudinal and not longitudinal, *Opisthopatus* being related to the South American *Metaperipatus* Clark, and *Peripatopsis* to *Paraperipatus* Willey of Notogea (see Brinck *op. cit.*).

A SYNOPSIS OF THE PATTERNS SHOWN BY THESE GROUPS

In Fig. 7 all the distribution patterns are shown together, the records for *Opisthopatus cinctipes* being omitted. Probable localities in the Eastern Highlands, where at least some of the aforementioned groups are likely to occur, are shown by hatching. Suitability of a locality was decided on the basis of field experience and a consideration of the following factors:

- (a) Altitude: at Cathedral Peak in the Natal Drakensberg the distribution of the faunal components has been investigated; here the lowest limit to which the palaeogenic elements occur is about 7,600 ft., except those groups with aquatic larvae which range down to 4,500 ft. where stream conditions permit.
- (b) Relief: relative relief is obviously important, since prominent topographical features tend to have a higher rainfall than surrounding lower country; cases in point are the Amatola and Zuurberg Ranges.
- (c) Aspect: east-facing slopes are more suitable because of their higher rainfall.
- (d) Rainfall: from a consideration of distribution records it seems that the 35-in. isohyet is of at least local significance.
- (e) The distribution of the Stormberg Volcanic Series: this series of lavas is responsible for the altitude and relief of the highlands of Basutoland and the fringing Escarpment, and of the high country between Barkly East and Elliot to the south of that territory. The lower level of the series is never below 5,000 ft. (du Toit, 1926). In the western part of Basutoland there is approximate coincidence of the fringe of this series with the 35-in. isohyet. In its central part Basutoland has been deeply eroded by the Orange River drainage whose valleys lie in rain shadow.

The overall distribution of the palaeogenic elements considered here thus includes the ranges of the Cape Fold Mountains and the Eastern Highlands as far north as the end of the Transvaal Drakensberg. This pattern seems characteristic also of other palaeogenic groups such as Plecoptera (Balinsky, 1956; Barnard 1934; and unpublished data), the Odonata *Chlorolestes* Sélys, *Ecchlorolestes* Barnard and *Presba* Barnard (Brinck, 1955), various genera of Ephemeroptera (Barnard, 1932, 1940; Crass, 1947), and genera of Myriopoda and Opiliones (Lawrence, 1953). It fits as well primitive groups which have entered South Africa from the north sufficiently recently to be represented still by relict species on tropical mountains or highlands in Africa, examples being carabid beetles of the genus *Plocamotrechus* Jeannel (Basilewsky, 1958) and turbellarians of the genus *Cura* (Marcus, 1955). In many respects the same pattern is shown by members of the Cape Flora (see Weimareck, 1941), a resemblance in distribution due perhaps in some cases to a direct association with that Flora, but in other cases to a dependence on a similar set of ecological requirements. In fact it seems that this pattern is widely applicable, and thus worth a brief examination in more detail.

The range of the montane palaeogenic elements falls into two parts, for which the terms *Cape Centre* and *Eastern Highlands Centre* are suggested (indicated in Fig. 7 by A and B respectively). This is not a complete division as it is not relevant to all groups.

The Cape Centre: This comprises the Fold Ranges of the Cape System, the approximate northern limit of which is shown in Fig. 7 by the heavy line. The ranges fall into two groups (du Toit, 1926; King, 1942), a slightly older western group trending north-south, and a more elongate southern group trending slightly south of east. These groups intersect in a complex manner in the south-west Cape. Within the Cape Centre distribution is determined largely by rainfall consequent upon relief and aspect, and the effects of rain shadow are profound.

The zones favourable for montane palaeogenic elements are restricted and narrow, and generally only the summits and seaward slopes of the ranges are suitable. In places, as in the Tsitsikamma area, these elements are found in forests on the coastal plateau or in river gorges seaward of the mountains. Species in some genera, for example *Peripatopsis* (Brinck, 1957) and *Ecchlorolestes* (Brinck, 1955), show a tendency to fall into eastern and western assemblages within the Cape Centre. The western group of Fold Ranges and the region in which the two groups intersect are in the winter rainfall zone, and it is here that there is the extraordinary concentration of palaeogenic elements that has attracted so much attention. For a high proportion of elements the eastern limit within the Cape Centre is Algoa Bay. The eastern extremity of the Fold Belt, comprising the Zuurberg and country around and to the east of Grahamstown, is apparently much poorer in palaeogenic elements, and its significance will be discussed below.

The Eastern Highlands Centre: As can be seen in Fig. 7, this falls roughly into three subcentres.

(1) The Basutoland—Drakensberg Highlands and Eastern Plateau Slopes: an extensive area suitable for palaeogenic elements but as yet little explored. Basutoland and the high country to the south, built by the massive pad of Stormberg lavas, are occupied today by alpine grassland; the Cape macchia is represented but is not a dominant floristic component (Weimarck, *op. cit.*). At the highest altitudes there is a noticeable impoverishment of the flora which shows as well many morphological changes in response to cold, poor soil and altered composition of sunlight (Schelpe, 1946). In the Natal Drakensberg, palaeogenic elements with aquatic immature stages, such as Blepharoceridae and Megaloptera, are to be found as far down as 4,500 ft. where stream conditions are suitable, and upwards right to the extreme headwaters where these rise on the lip of the Escarpment, sometimes showing species-succession with increasing altitude (as in Blepharoceridae). On the Plateau Slopes these stream-breeding groups are widely scattered but in a more or less definite pattern, being almost invariably distributed along scarps bordering elevated remnants of the Miocene Penepplain, cut by the cycle of erosion initiated by uplift in the mid-Miocene (see King and King, 1959).

Among grassland insects there are relatively few palaeogenic elements up to about 7,000 ft. at Cathedral Peak in the Drakensberg, and most of the species are common Midlands ones or range even further afield, but above about 7,600 ft. a change is evident. Flowering plants become more abundant, especially *Scabaeus* and many species of *Helichrysum*; with increasing altitude the number of the lowland insect species decreases precipitously and there is a concomitant acceleration in the number of endemics. Close to the crest of the Escarpment, above 9,000 ft., both fauna and flora are greatly reduced in species, but these are now almost all endemic and many belong to palaeogenic groups.

Montane forest cannot be dealt with at length here; reference should be made to Lawrence (1953) and Acocks (1953). It has its upper limits at about 5,000 ft. in the Drakensberg and at numerous localities on the Plateau Slopes. This forest is now scattered in many relief patches, but the conclusion is inescapable that these were formerly much more extensive and commonly continuous with one another. The distribution of the forest element generally is likely to be best understood on the basis of the probable original extent of forest as shown in Acocks' (1953) Map No. 1.

(2) The Amatola Range: This is built of Karroo rocks, and is an outlier of the high country at the southern end of the Drakensberg. The Amatolas probably became an independent physiographic entity after the mid-Miocene, as they are isolated by the valleys of the Great Fish and Great Kei Rivers which cut back and became deeply incised in soft Ecca Shales after regeneration following elevation in the mid-Miocene and in subsequent

cycles. Nevertheless this Range must have been a feature of fair relief before that time as its summits are well above the present-day level of the Miocene Peneplain.

(3) The Eastern Transvaal Subcentre: As far as is known at present, this is restricted in extent, occupying the Transvaal Escarpment as far north as the Tzaneen area, and the elevated country around Barberton. Only stream-breeding and silvicolous palaeogenic elements occur here.

The significance of these subcentres for speciation varies from group to group. In Blepharoceridae speciation has been very active. This may have been due to a more complete subcentral division of the mountain stream biome by the absence of a well-defined Escarpment in the Middleveld area (see King, 1942); here the Miocene Peneplain of the Highveld slopes to the Lowveld, though with much local relief. Whether this is true for other stream-breeding groups is uncertain. In silvicolous groups many examples could be provided of closely allied species in the forests of Natal and the Eastern Transvaal subcentre, though in other groups the same species occur throughout. Acocks (1953) distinguishes the forests of the Eastern Transvaal subcentre and those of Natal as different floristic types, Inland Tropical Forest and Temperate Forest respectively, so there may be an ecological basis for speciation within these subcentres.

Shown also in Fig. 7 are the Eastern Highlands of Southern Rhodesia. These mountains are known to have some palaeogenic elements that have obviously entered from the south, though the number is small. Examples have not been provided by the groups considered above, but are to be found in *Lampromyia* Macquart (Stuckenberg, 1960a) and *Chlorolestes* Sélys (Pinhey), 1951).

Intervals in the Pattern: At the extreme eastern end of the Fold Belt there is an area transitional between the Cape and Eastern Highlands Centres. This comprises mainly the Zuurberg and mountains around and to the east of Grahamstown. At present it is isolated climatically, on the north side by the dry Fish River valley, and to the south-west by an arid zone extending from the interior to the shores of Algoa Bay. There are two areas of maximum precipitation, one on the Zuurberg and the other to the east of Grahamstown, in neither case exceeding 35 in. p.a. The Uitenhage basin, which lies between Port Elizabeth and the Zuurberg, formerly had a rugged topography, but this was submerged beneath marine deposits laid down by a marine transgression which penetrated far into the basin during the lower Cretaceous (du Toit, *op. cit.*). During the Tertiary a second but less extensive marine transgression deposited the Eocene-Pliocene Alexandria formation over part of the Uitenhage basin and eastward termination of the Fold Belt, and must have affected the suitability of the region for palaeogenic elements. This transition zone is relatively depauperate, most of the Cape palaeogenic invertebrates stopping west of Port Elizabeth, and few of the Eastern Highlands elements crossing the Fish River. It is transitional for example in Onychophora (Fig. 6), certain Ephemeroptera (Crass, 1947) and probably Plecoptera (Balinsky, 1956: and unpublished data). In some respects the Amatolas are part of the transition region as well, as there is a number of examples of groups which extend from the Cape Centre no further north than the Amatolas. A good example is provided in Opiliones: in the genus *Larifuga* a series of species extends from the Cape Peninsula to the Amatolas, while the related genera *Larifugella* and *Adaeulum*, have an eastern distribution, just crossing the Fish River valley to the south and extending to the Eastern Transvaal subcentre in the north (Dr. R. F. Lawrence, *personal communication*). The Great Kei River valley, deeply incised, and occupied by Valley Bushveld (Acocks, *op. cit.*), clearly is a barrier comparable to the Great Fish. In Acocks' map of Veld Types (Government Printer, Pretoria, 1951) macchia (subdivided as False Macchia, No. 70) is shown to extend from the west over the transition zone at the end of the Fold Belt and to

be checked by the arid Fish River valley and its Valley Bushveld (No. 23). Evidently there is a natural floristic boundary here as well.

The most significant interval of all is the Limpopo valley, which delimits in a decisive manner the northern distribution of many palaeogenic invertebrate groups. This is an ancient trough since Jurassic and Cretaceous faults border it on the south against the Zoutpansberg. It interrupts widely the Escarpment and its Mopani and Bushveld are almost a complete barrier to stream-breeding and silvicolous palaeogenic elements occurring on the Transvaal Drakensberg. This low-lying tract has been a highly efficient ecological barrier far back into the Tertiary.

CONCLUSIONS

As a result of more extensive collecting in recent years it has become apparent that many of the montane palaeogenic invertebrates formerly known from the south-west Cape have a wider distribution. Many of these have been found in mountainous parts in the east and north-east of South Africa. The distribution pattern shows two main centres, a Cape Centre and an Eastern Highlands Centre, the latter with three sub-centres, as described above. The Cape Centre is the richer of the two in species, frequently richer in genera, rarely in families, amongst the examples considered and among others in the literature. This richness in species, and therefore probably the greater number of genera, is clearly due to the presence of an extraordinary combination of factors promoting speciation in the Cape Centre. Among these factors might be mentioned the antiquity of the landscape, the folds being post-Ecca and pre-Cretaceous, with a recrudescence of faulting in mid-Cretaceous (King, 1942); the varied nature of the topography, mountain ranges of considerable relief though relatively low altitude rising abruptly from a flat coastal plain or intermontane valleys, incised transversely by deep poorts and longitudinally by old established drainages, features which initiate allopatric speciation; the floristic trichotomy of forest, macchia and karroo vegetation, three competing floras, the macchia often being associated with montane palaeogenic elements and having undergone frequent rearrangement in response to climatic change (Weimarck, *op. cit.*); and the climate, characterized by winter rainfall in the south-west and more or less perennial rains east of the Gouritz River, the zones of high rainfall being confined to the summits and sea-facing slopes of the Fold Mountains, with marked rain-shadow effects in the intermontane valleys.

It is the opinion of the author that the Cape Centre is not to be regarded because of its faunistic wealth as the node from which palaeogenic elements have spread to the mountains in the north-east. The occurrence of these elements in the Basutoland-Drakensberg Highlands is instead considered an original feature of a very old distribution pattern. This opinion is based on the following observations. Firstly, these highlands are an ancient physiographic entity (see King, 1942). They owe their existence to the cap of Stormberg lavas which are resistant to water erosion. The lavas were extruded in the early Jurassic, and after being folded to the east in the Natal Monocline, must have been subjected to river erosion, at which time the present drainage pattern evolved and when the Drakensberg Escarpment must first have been formed. This Escarpment has thus been continuously present since late Jurassic times. It was unaffected by the rise of the Cretaceous seas which drowned parts of the Cape Centre. In fact, the Basutoland Highlands were one of the few remaining areas of high ground suitable for palaeogenic elements, persisting at the close of the planation of the continent in the mid-Miocene. Secondly, the last occasion when these Highlands were sufficiently continuous with the Fold Belt to share a common fauna must have been before the separation of the Amatola Range (i.e. mid-Miocene at latest). It must also have been during a time when conditions were favourable for a wide distribution of temperate montane forms, which was probably not during a cycle of planation but during or subsequent to a period of

elevation of the continental rim relative to sea-level. The latest available opportunity for this would seem to have existed in the late Cretaceous (see Dixey, 1955, and further references given by him).

It may be objected that this view cannot be correct since the Cape Flora, although possessing many features in its overall distribution pattern very like those outlined for palaeogenic invertebrates (see Weimarck, *op. cit.*), obviously is centred in the south-west Cape. The evidence for this location is impressive; according to Weimarck (p. 98) the Cape has four endemic families, 212 endemic genera and 3,536 endemic plant species of the Cape element, whereas only 347 species, not all endemic, are found in the Drakensberg. Probably the answer is to be found in the former distribution of forest, which is a potent competitor of the macchia vegetation. In Acocks' Map No. 1 forest is shown to have formerly restricted the macchia to the group of western Fold Mountains, the region regarded as the centre of distribution of this Flora. Its representatives on the Drakensberg have probably been derived from there during periodic contractions of the forest during climatic changes, and doubtless by means of chance immigration as well. In the south-west Cape the macchia underwent an explosive local evolution, far exceeding that of the fauna, but this must be seen as a special feature of the area.

This is essentially a preliminary study. A better understanding of the distribution of the montane palaeogenic elements can be possible only after a great deal of further collecting and taxonomic endeavour. More ecological investigations are also required as these must play a major rôle in the elucidation of factors controlling the dispersal of our palaeogenic invertebrates, notably as regards stream-breeding insects since we are concerned in their case with a zoogeography of immature stages. It seems safe to predict that more of these animals will be found in the Eastern Highlands, especially Basutoland and the Drakensberg. The prospect is exciting.

SUMMARY

The palaeogenic invertebrates are among the most interesting and distinctive animals in the South African fauna. This paper is an attempt to investigate the distribution of those that are confined to mountains. The distribution patterns of certain genera of Diptera, the Megaloptera, Onychophora, some Coleoptera and a Dermapteran are used as examples. The patterns show two main areas occupied by these invertebrates, a *Cape Centre* (the Cape Fold Mountains, especially in the south-west Cape) and an *Eastern Highlands Centre* (the Amatola Range, Basutoland, Natal Drakensberg, Eastern Plateau Slopes and Eastern Transvaal Escarpment). At the eastern end of the Fold Belt and southern end of the Eastern Highlands is a transition zone between the Centres, created partly by an arid tract of marine sediments extending inland from Algoa Bay and by ecological conditions unfavourable to montane forms in the Great Fish and Great Kei Valleys. The Limpopo Valley delimits the palaeogenic elements in the north, and is a major ecological barrier. It is considered that this pattern is a primitive one.

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DISCUSSION

- Prof. Balinsky:* The speaker mentioned that the paleogenic fauna is composed of three elements, namely silvicolous groups, groups with aquatic larvae and groups of the Cape macchia. He gave us a clear idea of the first two but not of the third.
- Dr. Stuckenberg:* This was for lack of time. Some are mentioned in the written paper.
- Dr. Harrison:* Amongst aquatic groups we have found montane species extending to the Drakensberg and Nyasaland, and, amongst Mayflies and Chironomids, even to the mountains of Abyssinia. Collecting is often very sparse but the distribution follows a pattern very similar to that shown by Dr. Stuckenberg.
- Dr. Bigalke:* It is interesting that there are even mammals such as the Bontebok and Bloubok, which are endemic and restricted to the South-west Cape.
- Dr. Stuckenberg:* I feel I should emphasize a fundamental distinction here. Practically all the vertebrates in the South-west Cape can be derived from tropical fauna; but the significance of these paleogenic invertebrates is that they are limited to the tips of the southern continents. They have few near affinities and such as they have are latitudinal not longitudinal. In Africa they have no northern relatives from which they could be derived.

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The significance
of cave-living animals
in the study of zoogeography

It may seem somewhat paradoxical to begin an account of animal distribution by a reference to cave animals, which have by far the most isolated and circumscribed habitat of all the ecological communities: nevertheless a comparison of the cave habitat with those of the open lands seems to me to have some bearing on the problems of animal distribution.

Professor Louis Fage (1931) in an important study devoted to cavernicolous spiders has developed some very interesting ideas as to the origin of cave faunas. These and further confirmatory researches have recently (1954) been ably summarized in a publication issued by that remarkable centre for research on cave and subterranean faunas, Le Laboratoire Souterrain de Moulis, situated on the Haute Garonne, France. I have taken leave to quote the relevant parts of this summary in the following paragraphs.

Professor Fage's ideas were based on the researches of Mayer and Plantefol (1925) which deal with the physiology of respiration in mosses; these biologists established the fact that the respiratory processes became more feeble as the water content of the mosses was raised. Applying this principle to cave faunas, Dr. Fage concluded that animals that live in an atmosphere with a saturated humidity show a very low rate of oxidation. The most striking characters of cave animals are blindness and absence of pigmentation, the latter having been previously ascribed to the fact of the cave animals living in darkness, but we now know that the formation of pigment is essentially the result of oxidation of organic matter (tyrosine, dopa) acted upon by oxidizing diastases (tyrosinases, dopaoxydase). It is now also understood that a lowering of the rate of respiratory exchange entails a diminution of melanin formation and, in extreme cases, its disappearance.

Work on both aquatic and terrestrial cave animals by W. D. and M. P. Burbank and Edwards (1948) in the U.S.A. and L. Derouet (1949, 1950) in France has shown that though cavernicolous animals are as sensitive to the reduction of oxygen in either water or air media as those living in the open, their respiratory metabolism is about three times lower as measured by oxygen consumption; the respiratory exchange of cave dwellers is thus distinctly inferior to that of forms related to them but living outside of caves. This falling off in the respiratory activity of cave animals finds an echo in their general behaviour; their movements are slower than those of animals in the open, the males are not so pugnacious. In Professor Vandel's words "the cavernicolous species are old, not only from the phylogenetic but also from the physiological point of view". Of the three principal factors

operating on cave animals, high humidity, darkness and a uniform temperature, humidity is by far the most powerful and is in the main responsible for the modifications so characteristic of cave species, viz: lack of pigment, partial or total disappearance of the eyes, reduction of chitination and the elongation of their bodies and appendages; uniformity of temperature and darkness, it is thought, play a subsidiary part which may be the non-activation of the oxidizing ferments in the absence of light.

The members of the large ecological group of cryptozoa which are found chiefly among the Arachnida, Myriopoda, Onychophora and Apterygote insects are also greatly affected by these three factors which however do not play as fundamental a part as in the case of the cavernicolous faunas. The cryptozoa may be said to occupy an intermediate position in these respects between the animals of the open and the trogllobionts, while sharing with the latter the limitations of a metabolism that is dictated by humidity more than by any other single factor. The microfaunas of forests are mainly found in the humus-covered substratum and therefore occupy a double habitat or rather one habitat, the forest humus, enclosed within a second habitat, the forest itself, both providing an atmospheric mantle with a high, constant humidity and uniform temperature. When occurring in more open regions the cryptozoa live under stones or in crevices of soil which provide microclimates with fairly high and uniform humidities.

The cryptozoa share the poverty of vision of the cave faunas. Many have small or feeble eyes while large numbers have none at all. Thus in a general population of crypto-fauna, such as can be assembled in a sackful of humus from the forest floor, the majority of the total numbers of individuals are blind. In contrast no insects, Arachnids or Myriopoda which live in the open have produced an eyeless form.

It is one of the interesting features of the crypto-fauna that in each class or subclass there is at least one large order or even suborder, which consists entirely of eyeless forms; thus the Chilopoda have the suborder Geophilomorpha, the Diplopoda the Polydesmoidea, while in the Arachnida there are several orders, the Ricinulei, the Palpigradi, and the Oribatoidea among the mites. These are large groups consisting usually of hundreds of species and confined in each case to a clearly differentiated order or suborder. In the cave faunas the case is very different, the blind species consisting of a few isolated forms, usually related to normal species living in the open or connected with these by various gradations of eye reduction.

This relationship between cavernicolous species and normal ones living in close proximity to them can be illustrated by three interesting South African examples belonging to three quite different groups of arthropods found on Table Mountain, Cape Town, where the well known Wynberg Caves occur in water eroded sandstone. The normal Cape Peripatus, *Peripatopsis balfouri* is closely related to the blind and unpigmented *P. alba*, the Pseudoscorpion *Chthoniella heterodonta* to the eyeless species *Ch. cavernicola*, the Opilionid *Purcellia illustrans* to *Speleosiro argasiformis*. In each of these orders the first named species can be found living just outside the openings of the cave in which the second species occurs. The trogllobiont Peripatid and false-scorpion differ from their cryptic relatives in being eyeless, while the Opilionids belong to a suborder of predominantly blind forms, both being eyeless.

This pervading condition of eyelessness in large groups rather than in individual species points to the fact that the cryptozoa have a very ancient history during which the absence of eyes has had time to become stabilized and crystallized in major taxa. Their origins and ecology can probably be connected with the earliest forest associations in the Carboniferous and they provided the stocks from which the cave faunas have arisen as specializations on the one hand and on the other the more modern insects and the families of spiders which now live in the open. The change led to complete isolation on the one hand of the cave

faunas, to the reverse in the case of the insects and other modern classes.

From the viewpoint of their humidity requirements it might be useful to divide all terrestrial animals into two chief categories and attempt to summarize the differences which separate them. Such an attempt is understandably of a very general nature which must perforce ignore the many halfway or intermediate types which cannot be easily accommodated in either of them.

Animals of the open lands are those which can tolerate wide ranges and changes of humidity, temperature and light; they have the ability to adapt themselves to a wide range of these conditions and are equipped with balancing or regulatory mechanisms in their respiratory and vascular systems. They have developed some sort of dermal covering such as a thick waterproof exoskeleton or cuticula supplied with pigment which prevent undue loss of moisture and heat by evaporation. They are thus able to withstand the direct impact of sunlight and are active animals able to disperse themselves over long distances by their own bodily exertions. To this division belong the higher winged insects, and, among the terrestrial vertebrates, the more recently evolved mammals and birds with a high dispersal potentiality.

The cryptozoic animals lack almost every one of the features listed for the animals of the open lands or are negative in these respects. They require the highest categories of humidity and a reduction below saturation point is often fatal. Both temperatures and light intensities are extremely uniform in the microclimates of their habitat, and the range of all three factors is extremely narrow. Their respiratory systems are of a very simple nature and are deficient in lacking regulatory mechanisms; in particular there is an almost complete absence of the highly developed and complex occlusory mechanisms of the pterygote insects which, by means of an elaborate muscular system, regulate the closure of the spiracles and enable them to prevent water loss by evaporation. The most typical examples entirely lack a well chitinized protective cuticle which, as in cave animals, often contains no pigment at all. They are thus unable to withstand the direct impact of sunlight on their bodies or the dessicating effects of air movements in the open and are confined by the nature of their structural deficiencies to the micro-environment in which they live. From the point of view of distribution they have a low dispersal potential and are in general static animals.

In times of catastrophe, such as the destruction of their habitat by a sudden lowering of humidity or a forest fire, annihilation is as complete as that caused by the eruption of Krakatoa; none can escape, no remnant is left to perpetuate the stock elsewhere in more favourable circumstances, as would be the case in vertebrates or insects. Those that have survived have been called by various names such as the relict faunas, archaic or palaeogenic elements, groups which must have persisted with little change over great periods of time.

In speaking of this cleavage between cryptic and other terrestrial animals in respect to their humidity requirements there are naturally some groups which do not strictly fulfil the conditions set out in the definitions given above but fall between them, while all the large classes of arthropods have some members of both the divisions. In the insects for instance there is a vast physiological difference between the higher winged orders and the apterygote insects at the other end of the scale which in groups like the minute Protura and endotrophic Thysanura (*Campodea* and *Japyx*) have all the distinctive characters of the cryptozoa, absence of eyes, lack of pigment or a thick cuticle. Both are insects but in their respiratory physiology and ecology are fundamentally different and for purposes of distribution cannot be treated under the covering term of insect.

The dispersal potentialities of various orders and suborders within the same class may be very different, being dependent on basic dissimilarities of organization, often with respect to the structure of their respiratory systems; some of the large Diplopoda with their powerful body armour live largely in the open while the small, thin-skinned orders pass their whole

lives in the shelters afforded by wood debris and soil. Among the Arachnida many of the more familiar families of spiders live in the open like the insects, indirectly dependent on the vegetation on which they spin their snares; most families however are invisible to the collector and completely cryptic in habit.

The scorpion and the solpugid are both Arachnids which flourish in deserts. The scorpion is a slow-moving nocturnal cryptic animal existing in burrows or in the humid atmosphere prevalent under large stones, with a comparatively simple respiratory system based on four pairs of lung-books. The Solpuga on the other hand is an arachnid with habits and movements more like those of many roving predaceous beetles which run over the desert sands, but is capable of even more rapid movement. It excels all other Arachnida in the efficiency of its respiratory system, being equipped with a vast elaboration of very wide tracheae while the chitinous ring-like openings of the spiracles are controlled by occlusory muscles. It further differs from its sister orders in having adopted the abdominal breathing movements typical of insects. Although both scorpion and Solpuga are desert living arachnids, the respiratory exchange measured by the oxygen consumption of the latter is many times greater than in the former. According to the degree of activity of the various groups and the accessory means used, such as the ballooning habits of certain spiders, the means of dispersal is modified and their distribution influenced.

This division, based chiefly on the presence or absence of regulatory and balancing mechanisms in the respiratory systems of animals and on the humidity factor, provides a physiological rather than a physiographical basis for the great differences in the manner of distribution of animal groups and the actual pattern of distribution which they reveal at the present day.

That there are differences in the distribution of the older cryptic animals and the more modern classes, both vertebrate and invertebrate, is fairly obvious and many authors have noted them for different groups of animals and plants. When Richard Hesse in his book "Tiergeographie" says that the fauna of Africa south of the Sahara exhibits a striking uniformity, he could have been speaking only of the higher categories of vertebrates and insects or of some special members of other invertebrate classes. With regard to the cryptic invertebrates, the reverse of Hesse's statement would be nearer the truth as will be seen from the examples which follow.

In the homogeneous arachnid order of Opiliones all the members live in forests and are with a few exceptions cryptic in habit; about 80 per cent of all tropical African species belong to one family, the Assamiidae. But in South Africa 78 per cent of the fauna belongs to another quite different family, the Triaenonychidae. In the tropics of Africa therefore the Assamiidae are completely dominant, in temperate South Africa the Triaenonychidae; no species of the former occurs in South Africa, or of the latter in tropical Africa. The cleavage of the faunas is thus complete, the boundary between them being represented by the valley of the Limpopo River. In respect of these two families the fauna of Madagascar also differs completely from that of tropical and subtropical Africa lying in parallel latitudes but is in strong agreement with the fauna of temperate southern Africa.

In another suborder of Opiliones, the Cyphophthalmi, the contrast between the faunas is even more marked. Six species of this small primitive group of blind harvest-spiders live at the extreme southern end of Africa, divided between two or three genera in the subfamily Sironinae. The only other African forms are two species of *Ogovea* and one of *Paragovia* in French West Africa, completely isolated from the other members of the suborder, both geographically and phylogenetically, and belonging to another subfamily, the Stylocellinae. The similarity in the distribution of the African members of this suborder to that of the Onychophora is quite remarkable.

The Onychophora have a long geological history going back in time to perhaps the

Middle Cambrian with little change of organization or appearance. The homogeneous structure of its members in different parts of the world at the present day points to a very wide former distribution. At the present there are less than 60 living species accommodated in two families, all of them very similar in structure and organization.

The dozen species found in South Africa are isolated at the extreme south of the Continent, no others being found between the East Transvaal and the northern coasts of Africa. The one exception is a West African species of *Mesoperipatus* which belongs to a different family and has no relationship with the South African fauna. According to Brinck, there are two centres of distribution for the South African Onychophora, one for *Peripatopsis* in the south west Cape where the largest number of species occur (four in the Cape Peninsula itself), the other for *Opisthopatus* in Natal where there are two species. *Peripatopsis* extends from the Cape Peninsula to Natal, *Opisthopatus* from Port Elizabeth eastwards, fading out towards the north-east, only one species being found in the Southern half of the Transvaal and that rarely, while none occurs north of the Limpopo. The relationships of the South African fauna are not with the rest of Africa but with Australasia and the southern parts of South America.

These are homogeneous groups but in a larger and more heterogeneous class of Arthropoda such as the Diplopoda there are enormous differences within the groups themselves with respect to size, thickness of the cuticle and activity, so that distributional relationships between the central and southern faunas may be quite different in two given families or two suborders of this class. In the Polydesmoidea for instance, an order of small blind millipedes, the cryptozoic family Spaeotrichopidae is strictly limited to rain forests. This predominantly African family is represented by 15 genera in South Africa, one of them, *Gnomeskelus*, greatly exceeding all the others in range and number of species. There is one genus in Madagascar while five occur in Australia and Chile each, but not a single species in the whole of Africa north of the Limpopo River.

The situation is however quite different in another suborder of Diplopoda, the Odonotopygidea, which are larger, well chitinized, more active millipedes, well able to live outside of forests in grasslands and thornveld. The recent work of Kraus (1960) has shown that in this suborder only six of the 34 African genera live in southern Africa, the remainder in tropical Africa, all being different from the South African ones. Seventy species, or three-fourths of the whole South African fauna, is confined to a single genus *Spinotarsus* while all the tropical genera are on the other hand quite small, with an average of four species per genus. This seems to indicate that the north-south migration route of these millipedes is the normal one followed by active self-dispersing animals living in the open. The central African fauna with its numerous clearly separated genera but with comparatively few species in each is thus obviously older than that of southern Africa, the numerous species of the one genus *Spinotarsus* representing the end product of an evolutionary line which commenced in or passed through the tropics and has ended in South Africa.

In summing up, the position with regard to the dispersal of animals in Africa seems to be as follows: the more active groups which are able to disperse by means of their own bodily activities and which can easily endure wide ranges of humidity and temperature, of which the mammals among the vertebrates, the insects among the invertebrates are the most typical, have migrated through Africa along a north-south route, following for the most part the eastern side of the continent.

The more sluggish cryptozoic invertebrates can only exist in an atmosphere of high humidity and with uniform temperatures. Being unable to withstand the direct impact of sunlight they are confined to their micro-habitats and are static as regards dispersal. These are so-called relict forms, much older than the animals of the open lands and do not appear to have migrated in a longitudinal direction but to have had local centres of distribution

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at the extreme end of the continent. They have no particular relationships with the tropical African faunas or only distant ones and differ further in having distinct affinities with those of Australia, New Zealand, South America or Madagascar in approximately the same latitudes.

It might not be so difficult to explain the fact that various families of cryptozoa living at the extreme apex of Africa are more closely related to those of Australia, South America and Madagascar than to any African families of the same groups living north of the Limpopo. What seems more difficult to explain is why these families do not occur in Africa at all north of the South African limits while being well represented in southern continents separated from Africa by thousands of miles of ocean. If only these relict forms were to be taken into consideration, southern Africa would have to be redefined as a new zoological province or subregion outside the Ethiopian one and differing from it as much as the Mediterranean subregion at its northern extremity differs faunistically from the rest of the continent.

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GERTRUD THEILER

ONDERSTEPOORT.

The Sandtampan *Ornithodoros Savignyi*: an ecological puzzle and an economic problem

GENERAL GEOGRAPHICAL DISTRIBUTION

The Sandtampan has been recorded from the Sahelian Zone in provinces of Mauritania, Sudan, Niger (French West Africa); Northern Bornu and Lake Chad (Nigeria); throughout Tchad (French Equatorial Africa); Northern Kassala; Khartoum, Darfur, Blue Nile, Kordofan (Sudan); in the Western Lowlands of Eritrea and French Somaliland; in the Eastern Lowlands of Ethiopia; scattered throughout Italian Somaliland, though generally rare; Northern, Central and Coast Provinces (Kenya); and Northern Province (Tanganyika); Southern Bechuanaland; Southern and Central South West Africa; and in the North West Cape in the districts of Kenhardt, Namaqualand, Mafeking, Vryburg, Kuruman, Gordonia and Hay.

It is recorded also from North Africa from Egypt, Libya, Tunis and Algeria; from Yemen, Aden, Palestine and Iraq in the Near East; and from the drier parts of India and Ceylon.

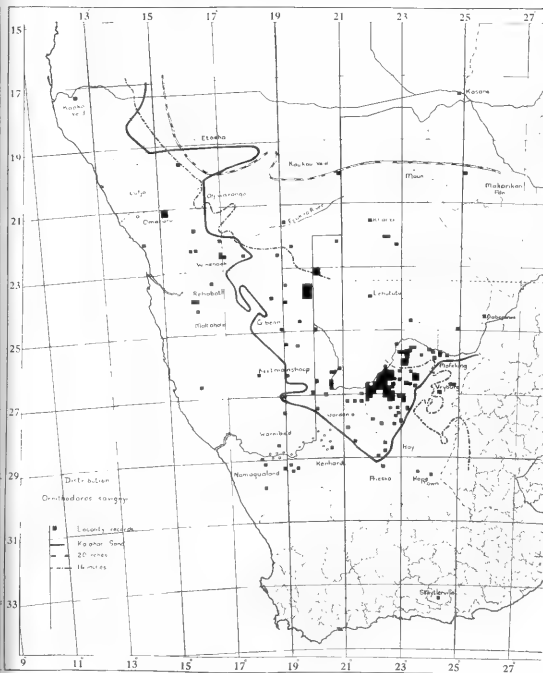
Hoogstraal (1956) expresses the opinion "*O. savignyi* appears to have erratically invaded Africa from the East . . . and part of its spread probably has been by camels, for in Northern Africa it is apparently most abundant [or through circumstances most frequently met with?] along camel routes". It would appear to me, however, that it has its origins in Africa, either in the dry Sahelian zones bordering on the Sudan, or in the Kalahari Thornveld of the North West Cape, of South West Africa and of Bechuanaland.

ANALYSIS OF ITS DISTRIBUTION IN SOUTHERN AFRICA

In an analysis of this sort, one must bear in mind that the records are most numerous for the populated areas and are necessarily scanty for the uninhabited areas. Also, with the increase in cattle ranching activities there seems to be an (apparent?) increase of tick activity, so that one must be wary of coming to the conclusion that the most thoroughly collected area is also the most heavily infested.

Fig. 1 shows *O. savignyi* to be present throughout north-western and western Vryburg; the western two-thirds of Kuruman, absent in the Langeberg Asbestos Mts. and Kuruman Hills; the western-north-western two-thirds of Gordonia; and spreading westwards and northwards into Keetmanshoop, Gibeon and Gobabis in South West Africa, all areas falling

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into the geological Kalahari beds and sand belt. Our records across the border for Bechuanaland are but few; possibly the tick is equally prevalent in the triangle between Khanzi, Bray and the western border ("both from Kuli and Nojane we could fill gallon tins from below big trees and from some cattle kraals"—Correspondence). The few records from western Hay connect up with south-west Kuruman. The tick is reported absent on the south side of the Orange River in Gordonia, Kenhardt, Namaqualand (Goodhouse, Dabenoris, Koenabib to Klein Pella and Haramoep-Wortel) and north of the Orange in Warmbad. It crops up again in the Bushmanland of western Kenhardt at Annakop, Samoep, Namies, Gams and in the Koupsleegte area, spreading westwards mostly in association with the Koa Valley dunes, into Little Namaqualand; and is said to be present throughout in the sands of northern Namaqualand (Wolftoon, Henkries, Droëdap) except for the west coastal strip. It is absent from the Richtersveld. As yet I have not been able to locate the two farms Abbots Dam and Wonderdraai, Hope Town district, from which the tampan has been recorded; and have but little information about the farm Allemanskraal in the Steytlerville district.*

In South West Africa it is present, and apparently abundant, throughout the Kalahari sand-belt of Keetmanshoop, Gibeon and Gobabis, up to the level of the Epukiro River (lat. $21^{\circ} 30' S.$), but absent in the Kaukaveld. Otherwise it is ubiquitous and exceedingly plentiful everywhere to the south of Rehoboth ($23^{\circ} S.$). It is also present in the west all along the Namib, though it is consistently absent from the Brandberg; as also from the shifting, shadeless southern dune belt, which extends from the Orange River to the Kuiseb River ($26^{\circ} 30' S.$).

North of Rehoboth it occurs sporadically in a belt stretching from the Windhoek district up to Omaruru ($21^{\circ} 25' S.$), with an odd record from Mopane veld near Outjo ($20^{\circ} 07' S.$). It appears to be absent from the Waterberg (not recorded by Sigwart in his careful survey of Outjo and Waterberg in 1914), and from Grootfontein, both of which fall mainly into the Kalahari sand belt. Thus far no tampan has been sent in for the Tick Survey from the Etosha Pan Game Reserve.

Dr. Martin (Geological Survey, South West Africa), who supplied much of the above information, assumes it "to be present throughout the Kaokoveld, as far as there are sandy soils". Thus far we have but one record from the extreme north west corner.

Some tampan has been sent in from Ovamboland (locality not given) with the statement, which I am a bit hesitant to accept, that "it is prevalent throughout".

In Bechuanaland the recorded areas lie west of Longitude 25° and South of Latitude $20^{\circ} S.$, except for an odd record from Kasane on the Chobe-Zambezi River.

RAINFALL AND CLIMATE

Most of the records for the North West Cape and for South West Africa are in areas with an annual rainfall of under 16 in. per annum. For Bechuanaland I have no figures, but as in northern Vryburg and the extreme north-west of Mafeking (according to the maps available) the records fall into areas with a rainfall under 20 in.

The South West Africa records show the sand tampan to be absent from the sub-tropical areas (Gobabis, north of $21^{\circ} S.$, and the Waterberg) and from the tropical areas (Grootfontein and possibly from the greater part of Ovamboland). These climatic conditions presumably are paralleled in the Kalahari sand belt of northern Bechuanaland and of the Caprivi Strip.

In French Equatorial Africa Morel reports it as abundant in the Tchad, with less than 20 in. of rain, throughout the Sahelian Zone; reported mainly from camel routes, 10 to 20 in.

* See Appendix.

VEGETATION

In the North West Cape the records fall mainly into the Kalahari thornveld proper, occurring on deep loose sand over calcareous tufu. This is very open savanna, with the trees *Acacia haematoxylon* and *A. giraffae*, *Boscia albitrunca* and the shrubs *Grewia flavia*, *Lycium hirsutum* and *Rhigozum trichotomum*, with sweet desert grasses, and with a basal coverage of slightly more than six per cent. The tick is absent from the other sub-division of the Kalahari sandveld, i.e. from the Vryburg Shrub Bushveld, which occurs mostly on rocky soils and which varies considerably according to geological formations (e.g. the mixed *Tarconanthus* veld of the Asbestos and Kuruman Hills, and the mixed *Tarconanthus*—Thornveld of the Langeberg and the *Tarconanthus* veld of Vryburg). It is also absent from areas where there is an invasion by the Karroo, as also from the Orange River Brokenveld. In Namaqualand it occurs mainly in the sandy areas of the Karoo-False-Grassveld, or False succulent Karoo. In Bechuanaland and in the Northern South West Africa, it dies out as the Mopane veld and its associated grasses replaces the Kalahari Thornveld.

KALAHARI SAND

The sand in the Kalahari may be 40 to 50 feet in thickness overlying a continuous sheet of calcareous limestones and grits, these rocks becoming richer in lime towards the top and generally exhibiting a hard crust of white limestone. These outcrops are met with in various parts, along the edges of the sand belt, e.g. the Urinanib plateau and adjoining regions in the south of South West Africa; the Koranna and Langeberg in Kuruman district, and in the Kaap plateau of Kuruman and southern Vryburg.

"Considering the vastness of the Kalahari region, the uniformity in texture is remarkable, the grain size rarely exceeding 1 mm., and ranging most commonly between 0.15 mm. and 0.4 mm., with the particles not very well rounded" (du Toit, 1939). The sand is alkaline.

For the Kaukaveld, however, it is stated that going northwards there is a change from sandy dunes to rolling plains of sandy loam. As yet I have no information on the sands of Namaqualand and South West Africa. *O. savignyi* is not found in the shadeless clayey soils of the pans.

TEMPERATURE AND HUMIDITY

In *O. savignyi*, according to Lees (1947), the critical temperature for water loss is 75°C (*R. evertsi*, 52°C). The usual wax layer on the skin is "reinforced" with cement deposits, giving a very tough though pliable skin. The cement probably consists of proteins tanned by quinones and intimately associated with lipides of some kind. (Wigglesworth, 1948).

We have no critical aridity/humidity figures, but that temperature and sunlight (apart from starvation) are not the only limiting factors was shown by experimental observations at Onderstepoort. Sandtampans kept at room temperature in shallow sand died very quickly; they survived somewhat longer under 5 in. but could not maintain themselves. If, however, the base of a 12 in. column of sand was kept moist the tampans could maintain themselves easily. They survived for several months in waterlogged soil. Another batch survived in desiccators at 10% to 50% R.H. at room temperature, and fed at the end of two months.

Lees and Beament have shown that unengorged ticks and tampans can take in water even against a moisture gradient, and can withstand being exposed to alternating periods of low humidity with periods of high humidity. The length of this period of adaptation is dependent, not only on the length of the times of exposure, but also on the starvation age of the tick. We have but little information on the starvation-survival-periods for *O. savignyi*, but it can be presumed that, as with most other "desert" Argasids under favourable humidity/tem-

perature conditions, for first stage nymphs it is a matter of six months to a year, or two, and for late stage nymphs and adults, from two years to five to eight years or more.

In *O. savignyi* in waterlogged soils it would seem that after a while the mechanism regulating water uptake breaks down, because a fair percentage were found to be so bloated as to have (presumably) died from bloat. This did not take place in moist soils, but only in very wet soils. Lees (1944) noticed inactivity of "wireworm" larvae exposed to high moisture in the soil. "The presence of excess moisture, however, also has the effect of inhibiting all muscular activity, this influences the manipulation of the mouthparts and locomotion alike". Possibly there is a similar phenomenon inhibiting the action of the muscles of the spiracle in the Sand Tampan. The temperature figures available to me for the Kalahari are 160°F at the soil surface (180°F for Namib); but at a depth of 2-3 in. the temperature is well below the lethal level for insects; and at a depth of 12 in. or more it remains fairly level not only during the 24 hours but also throughout the year"—(Correspondence).

According to Dr. Martin, "It was observed that Sand Tampans are destroyed if a dense stand of grass under a tree is burned down" and he wonders whether the frequency of veld fires in some areas may not be a limiting factor to the tampan's presence. However, in one experiment, pouring petrol over a kraal with manure, and setting it alight did not eradicate the tampan, which was still present quite near the soil surface after the fire had died down.

"In live dunes of the Namib, especially the large ones, there is a permanently moist bulk covered by a dry layer, which varies in thickness in accordance with the prevailing moisture conditions of the atmosphere; thus in dunes deeper inland this dry layer is thicker than in the Namib dunes in which it is often very thin indeed, the Namib atmosphere has a relatively high moisture content, with sea fogs and heavy dews. In the Kalahari the relative atmospheric moisture is very much lower, dropping to below 5 per cent as against 60-80 per cent in Namaqualand and the Namib at the same time of day"—(Correspondence).

At Mogadiscio (Italian Somaliland) *O. savignyi* is controlled by dampening the court-yards with sea water. It would be of interest to find out whether the deleterious factor is the moistness or the salt.

As yet, I have not plotted the West African, East African or Sudan records. In areas bordering on the Sahara—in the vegetational sudano-sahelian zone—it is possible that the tampan will occur in localities with a higher average annual rainfall. It must, however, be remembered that here the average temperature is possibly higher than in the Kalahari, and also that (in average years) the dry season is drier, due to the hot winds blowing from the Sahara during this time of year (Aubreville, 1960).

PREFERRED HABITAT

O. savignyi avoids exposed sites where the ground temperature may go up to 130°F. It occurs mainly in deep sand in the shade of large-crowned trees, especially the Kameeldoring *Acacia giraffae*. It is also found under the Vaalkameel *Acacia haematoxylon*, under the Witgat *Boscia albitrunca* and the Rosyntjebos *Grewia flava*, if these are large enough to throw good shadows in which animals can shelter.

According to Dr. Martin, "In drier parts of Greater Namaqualand and in the west all along the Namib the Sand Tampan is not confined to the sand-covered areas. It is just as plentiful under trees and bigger bushes in the mountainous tracts, as long as there is a thin veneer of sandy soil, which is practically the case under every bigger bush or tree. The clayey soils support, as a rule, no bigger bushes or trees. The tampan is never found outside the shaded area under a tree, but it is plentiful also in the sandy soil under the shade of rock shelters frequented by game. . . . It does not occur under trees growing in actual beds of dry river courses which are subject to occasional flooding".

It seems agreed that the Sand Tampan avoids sunlight and sand exposed to the direct

rays of the sun, as the sun travels so it follows the tree shade. At Khanzi (Bechuanaland) the farmers consider 25 yd. away from a large tree as a safe distance. Hoogstraal (1956) brings out this avoidance of sunlight very clearly. "At the Khartoum quarantine station one may see a long seething line of thousands of hungry Sand Tampans helplessly confined to the shade of a row of *Acacia* trees. A few yards away, separated only by the hot nine o'clock sun, newly arrived cattle tied to a post fence tempt the Sand Tampans to cross the glaring strip. The next morning in the coolness of seven o'clock those tampans under the trees are all blood-bloated and resting comfortably in the sand, others are dragging back from their hosts across the now non-existent barrier, and the legs of the cattle are beaded with yet other podshaped ticks taking their fill of blood, in a regular line just above the hoof".

In Italian Somaliland and in Berbera the Sand Tampan is said to occur in large numbers in "native huts" and courtyards. In these regions, the living unit is a hut, floor paved or unpaved, having a stone or mudbrick wall surrounding a sandy courtyard, in which the owner plus his fowls and stock all live together. These structures between them apparently offer sufficient shade for the Sand Tampan to maintain itself.

According to Hoogstraal, in the Sudan the tampan at well sides and in native corrals is but superficially burrowed. This would also be the case in the mountainous tracts and rock shelters in South West Africa. What the position is in the deep Kalahari sands of the North Western Cape, Bechuanaland and South West Africa is difficult to say. It has been found at levels down to nine inches. Laboratory observations indicate that it can, and will, go deeper than this.

The evidence in cattle kraals and in stock yards is often conflicting. Apparently it can maintain itself in these localities if the overlying manure is loose and not compacted, although some farmers state that it would seem that they do not like manure; possibly the thickness of the manure layer is a deciding factor. Whether the urine in the manure has any repellent or deleterious effect has not been ascertained.

SURFACE ACTIVITY

It is agreed that the Sand Tampan will feed equally readily at all hours of the day and night, though most farmers state that it is more active during day time. This observation is not above suspicion for (a) but few farmers are out during the night, and (b) cattle do not feel the need to sleep under trees at night time.

The information offered on seasonal activity is conflicting. It is generally agreed that the tick is most active in summer when it is very dry, and that it is not very prevalent immediately after good rains, although more than one farmer states that it appears during wet periods. "Unfortunately I was unable to send you the specimens required earlier because the recent rains, and the heavy dews at night, keep the sand damp, and what happens to the tampans when the sand is wet is a riddle to me"—(Correspondence). According to most observers it is more active during the warm summer than it is during the cold winter months. One farmer remarks: "It is very seldom that you see any large ones during winter. Small ones, however, are not wholly inactive. When the cattle are driven into the pens the smaller tampans are there, only not so many as in summer". Others mention that the tampan comes out on warm days in winter.

It frequently happens that cows that have calved under trees have lost the newborn owing to exsanguination overnight. One farmer lost several head overnight after placing his cattle in a kraal that had not been used for several months. In one instance up to three gallons of engorged tampans were collected alongside of three cows killed by exsanguination.

UNDERGROUND ACTIVITY

Under field conditions the tick has been reported from 3 in. downwards. How deep down it can go has not been established, but apparently it goes fairly deep, for often it takes five minutes or longer before any activity is seen on the surface of the soil. The tampan can travel quite quickly through loose dry sandy soil, but it has much more difficulty in moist soil when the sand particles adhere to one another.

Under experimental conditions it has been found embedded motionless in the moist region of a column of sand. However, it was not ascertained how long these ticks would survive these moist conditions—certainly a few months.

HOSTS

In that *O. savignyi* is a quick feeder it is difficult to establish a host list. It attacks large game, camels, dromedaries, cattle, mules, donkeys, sheep, goats and pigs and man quite readily. Lion, rhinoceros, buffalo and giraffe have also been listed.

Whether the movement of smaller animals is a sufficient stimulus to bring the tampan to the surface still is a moot point. Placing fowls under a tree in itself did not bring forth the tampan, but when the owner sat next to them, it came out quickly. This same observation has been made for small dogs.

Besides calves, kids, lambs and pigs may succumb to tampan bites, but it is not known whether these were by themselves, in a troupe or accompanied by a larger animal. We have no information about springbuck, and smaller animals or ground birds.

Although the sand tampan is a quick feeder (first-stage nymphs engorge in 10–74 minutes, later stage nymphs and adults in 15–30 minutes), it would seem that, nevertheless, it is entirely dependent on its host for dispersal. That this is so is shown by its prevalence in North Africa and elsewhere along camel routes where caravans have plied, or, are still plying; and in South Africa in sales stock yards. In southern Africa game may play a rôle; gemsbuck are frequently seen to stand in the shade of trees under which tampan bites are known to occur. However, if the sun is not too hot and if alternate shade is available they will avoid large trees.

STIMULUS

According to field and laboratory observations the tampan responds to soil vibrations very quickly. But often in the laboratory it has been observed to appear on the surface independently of any vibrations, and, since the jars of soil were under constant laboratory conditions, these appearances were independent of any increase in soil surface temperature, nor did these appearances show any constancy nor rhythmic hunger urges.

ENEMIES

Predators in nature do not appear to have been reported. Under laboratory conditions rats have been known to feed on nymphs and on adults. Mice commonly assault nymphs, but only particularly bold individuals attack adults. These rodents, in turn, easily escape blood-thirsty but lumbering adults, although small active nymphs more easily attach to them. One farmer states that since he has introduced guinea fowls onto his farm he has not been troubled by Sand Tampan. The question may be put whether in the more heavily populated areas, it is not only the increase in the food potential, but also, or rather, the decrease of the game birds, quail, guinea fowl, partridge, sandgrouse and francolins, which has led to the build-up of the Sand Tampan infestation. Domestic fowls have been seen feeding on the Sand Tampan.

DISCUSSION

Control

Any control method to be useful must meet the four requirements: (1) it must kill the tampan; (2) it must have a long residual effect; (3) it must not kill shade giving trees; (4) it must be economical and easily applied.

As yet we do not know the temperature and/or humidity preferences of the tick, but assuming that it likes a constant temperature and a fairly high humidity it would appear that it would be "at home" in the sand at a depth between 12-24 in. (30-60 cms.). At Mata Mata in the Gemsbok National Park air humidity at 5 p.m. falls to 9 per cent rising to 42 per cent overnight. In the Namib comparable figures are 35 per cent and 95 per cent, so that in the Kalahari the tick would normally burrow deeper down than it does in the Namib.

In so far as water is never abundant, insecticides in powder form, or as granules, would have preference over emulsions or wettable powders, as also over soil fumigants, which need a sealing layer of water.

If insecticides are to be used, to be economical, the less sand they are mixed with the better. Thus some method must be devised, not only to bring the tick to the surface but to keep it in the top few inches. This could be done by keeping the surface soil moist and "mild", possibly by the application of a thick layer of sawdust or of humus (scarce in the tampan veld), or possibly by spreading sheets of plastic in the shade of the trees, or possibly by the application of some water-holding clayey or colloidal substance (uneconomical and possibly harmful to the trees).

It would appear that fencing off the shade of trees and enclosing fowls that scratch, offers some hope of success. Starving out any tampan is almost an impossibility in that the starvation-survival periods are long. If *O. savignyi*, for which we have but scant information, runs true to tampan form it can stay without food for quite a few years.

Changing grazing and animal husbandry practices, it appears to me, should help considerably. On many farms the cattle range during the night and are coralled by day. In the course of time, hence, the kraals, positioned at the waterpoints, become heavily infested, the cattle providing the shade necessary for the tampan during the day. In some instances the cattle range by day and are coralled at night. During the heat of the day the cattle seek available shade and are attacked. Either way, they meet up with the tampan. Carting water over the sandy stretches would be uneconomical. It would seem that the most feasible solution would be, in these days of plastic piping, that the day kraals and their water troughs should be moved from time to time and the manure in the old kraals removed leaving the kraal soil surface exposed to the sun. This would entail less work and wire than would fencing off all the shade trees on the farm/ranch.

Herding of cows-in-calf is indicated, with the provision of moveable shelters in a specially prepared camp, so that cows do not have to look for the shade of trees.

To await the advent of a guaranteed foolproof insecticide is courting trouble, whereas changing of grazing habits and introducing sound animal husbandry practices offers some measure of relief and of control.

ADDENDUM

A fleeting visit of one day (14.7.61) to Allemanskraal, Steytlerville district, since writing this article, has shown that the ecological background and the behavioural pattern of the tick in this area differs slightly from that in the North West Cape.

Allemanskraal, 33° 14' S., 24° 15' E., 1,400 ft. above sea level, in the Grootrivier Range, has an annual rainfall of 7-97 in. with a slight fall every month, the winter being drier than the summer. The average yearly temperature is about 66°F, rising into the hundreds during the seven

summer months, averaging a yearly minimum of 56°F with an absolute minimum of 30°F. Heavy frost is seldom experienced.

The vegetation is typical Noorsveld; "a uniform 4-6 ft. high scrub of clusters of grey, shrubby, succulent, spiny *Euphorbia caerulea* (Noors), dotted with small trees; the largest of these small trees are mostly the dark small-leaved *Pappea capensis* (the Pruim or Berg Pruim). Interspersed amongst the dominant Noors are various species of inconspicuous shrubs. In the shelter of these shrubs one can still find some Karoo herbs and grasses. Owing to the ability of goats to eat chopped *Euphorbia caerulea*, as a last resort during drought, this veld type has suffered particularly badly from overgrazing, and in its present condition is often seen dimly through a dust storm" (Acocks 1953). The soil at Allemanskraal is mainly clayey and is mostly beaten, or tramped, hard between the Noors clusters.

The Sand Tampan, according to Mr. Hayward's experience, borne out by our one day visit, is found under the larger *Pappea capensis* where there is a loose layer of soil. This layer in many instances is less than $\frac{1}{2}$ in. deep, in others it may be up to 3 in. Under no tree did we find any greater depth of loose soil.

Tick activity under the trees was variable; under some there was no response or but little response to our presence (*i.e.* trees known to harbour the Sand Tampan). Under one the response was so overwhelming that eventually we had to beat a retreat on to safe ground.

Invariably the first ticks to come above ground were the younger-stage nymphs; the larger nymphs and adults appeared much later. Some adults apparently travelled under ground, for they were only found at soil surface underneath where we had been sitting. Obviously freshly engorged Sand Tampans were found hidden very superficially either under a very thin layer of dust or under a few small dry leaves. As often as not the tampans were well beyond the shade of the trees. The air temperature was 71°F. The soil, however, was not hot to the touch.

In his experience, Mr. Hayward has not found the tick on either his cattle, goats or sheep, but he has found them on kudu, which frequently rest under the Pruim trees.

It is to be anticipated that the tick is to be found throughout the Noorsveld. That it has only recently been recorded from the area may possibly be explained by the herding practices (or the lack of herding practices) which obtain. Its abundance at Allemanskraal points to a long established presence.

The Steytlerville Noorsveld tampan is thus seen to show slight differences from the Kalahariveld tampan, in that it exists in shallow layers of sand, under smaller trees (just about big enough to offer shade to one resting Kudu) has no objection to a (temporary) appearance in the sun, and is active all the year round. The observation that it is the young stages that appear first, confirms the finding in other regions that it is the young that are most active.

Dr. W. G. Walton, writes to say that the Noorsveld tick shows a few slight taxonomic differences from the Egyptian tick.

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*I thank W. J. Hayward for the information supplied and for his hospitality during our short stay at Allemanskraal.

SUMMARY

The geographical distribution is given. Its distribution in southern Africa is analysed: here it is shown to be present mainly in deep sand, but may occur in shallow sand in rock shelters. In the North Western Cape it is mainly associated with the shade of *Acacia giraffae* and *A. haematoxylon* of the Kalahari thornveld; and in Little Namaqualand it is associated with the shade of the larger trees of the Karoo-false-grassveld. It occurs in regions having less than 20 in. rain per annum; it avoids direct sunlight, cannot exist in dry sand; it is not known to what depth it penetrates into the sand nor what its preferred pH is. Small animals play no rôle, or but a minor rôle as hosts; their weight and movements being inadequate to cause vibrations of the earth which appear to be the main stimulus to bring the tampan above ground.

Control measures. In view of the scattered distribution over a very large area, the depth of the sand and of the lack of water in these areas, measures necessitating the use of water are impracticable and uneconomical, thus ways and means will have to be found either (1) of changing the nature of sand, or (2) of bringing the tampions to, and keeping them at, the soil surface, where specific insecticides having long residual values could be applied and/or (3) of changing grazing habits and of introducing sound animal husbandry.

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DISCUSSION

Mr. Bateman: With regard to the effects of vibration, similar responses may be observed in other animals having an underground habitat. I have some evidence that golden moles may come to the surface when stimulated by small vibrations such as might be produced by earthworms. However, once on the surface, they seem to have no direction-finding apparatus but to search for their food at random.

Dr. Winterbottom: Have you direct evidence that Guinea fowl eat tampions?

Dr. Theiler: Some, yes.

Dr. Bigalke: In the Kalahari there is a big gap in the distribution of Guineafowl.

Mr. Attwell: Are there no other birds, such as the dry-country francolins, which might take over in the absence of Guineafowl?

Dr. Theiler: It is only a theory of mine that the increase in the tick may have accompanied the killing off of game birds.

Dr. McLachlan: Would it not be possible to control these ticks by bringing them to the surface by means of a simple vibrating device and then spraying.

Dr. Theiler: Very possibly, but there has been no work on such control methods in the field as yet.

P. B. N. JACKSON

JOINT FISHERIES RESEARCH
ORGANISATION,
SAMFYA,
NORTHERN RHODESIA.

Ecological factors affecting
the distribution of
freshwater fishes in tropical
Southern Africa

It is a *sine qua non* that, if a fish is to live, it must have water. It is not sufficient, however, to consider the distribution of freshwater fishes entirely in terms of the amount of water in the form of lakes, rivers, streams and marshes that are now, or have been in the past, available to make the existence of fishes in them physically possible. As well as the physical factors inherent in the sheer existence of water, there are also ecological factors which affect the distribution of fishes. I do not propose in this short paper to discuss very much the physical factors of the availability of water, watersheds, barriers and so forth. While much remains to be done, such aspects of the distribution have been discussed (for the area in question) by, among others, Worthington (1933), Ricardo (1943), de Beaufort (1951) and Poll (1957). Comparatively little is known, however, of the ecological factors involved, and it is the main purpose of the present paper to discuss some of these aspects.

The fresh waters of tropical southern Africa include two large Rift Valley lakes, Tanganyika and Nyasa, a series of smaller lakes, and a wide range of rivers, streams, swamps and marshes. Fishes are widely distributed in these, very often discontinuously, and it is clear that ecological factors play a large part in this distribution. We are very far from having even an empiric knowledge of each fish; when we do, many of the present difficulties confronting the student of distribution will probably fall away.

At the beginning of a fish's life, as egg, alevin or fry, it seems that the most important ecological requirements of this stage are cover, a refuge from predators, and food. The theory has been put forward by Jackson (1961b) that, in order to place the eggs and young in an environment where these requirements can be met, parent fishes undertake an annual spawning migration. Even in our present limited state of knowledge a list of such known spawning migrations is impressive. The movement is always upstream, and known migrations include both extended movements up large rivers into smaller tributaries, swamps and flood-plains, and also many cases of anadromesis from large lakes into affluent rivers. As Whitehead (1959) has remarked, migrating fishes must have the ability to tolerate a wide range of environmental conditions, such as, in the case of anadromous fishes, those that exist between river and lake.

It can be seen that we have here a case where ecological factors can affect distribution. While the urge to migrate may be primarily for spawning and, according to Jackson's (1961b) theory, motivated primarily by the powerful urge to place the eggs and young in an environ-

ment most suited for their survival, it can readily be seen that the very fact that such a strong migratory urge exists is in itself a potent mechanism for the distribution of freshwater fishes. Species of fish which undertake long and often arduous migrations at regular intervals are *ipso facto* in a good position to colonize new waters when these become available, as, for example, when a river changes its course or a barrier breaks down in the course of geological time.

The position of such migratory species may be contrasted with that of the species which exist, often in species-flocks of closely related species, in the Great Lakes of Africa, such as (in the area under review) lakes Nyasa and Tanganyika, and are endemic, each to a particular lake. It is a remarkable fact that these endemic species do not migrate out of the lake up rivers to spawn to anywhere near the same extent as do those which are either non-endemic or are closely related to a more widely distributed species. In discussing this phenomenon with regard to the anadromous fishes of Lake Victoria, Whitehead (1959) has this to say (p. 343): "Amongst the anadromous fishes of Lake Victoria speciation nowhere approaches the level found for example in the static cichlid species of the lake. The anadromous fishes . . . are able to overcome large micro-environmental barriers in temperature, substrate, feeding possibilities, etc., barriers which appear to isolate many of the more specialised lake forms."

It thus seems possible to reach the following conclusion with regard to the distribution of fishes in tropical southern Africa. This is that distribution over wide areas of the sub-continent is limited to those unspecialized fishes of migratory habit which are not endemic to a lake. The narrower ecological requirements of the lake endemics appear, in our present state of knowledge, to make it impossible for them to distribute themselves in any water, no matter how adjacent, other than that lake to which they are endemic. There are dozens of genera and hundreds of species, especially though not exclusively of the family Cichlidae, known from Lake Tanganyika and Lake Nyasa, but, apart from those anadromous fishes closely related to species outside which are mentioned above, no records exist of any of these endemics being found in rivers, marshes, etc., even where no large barriers exist and non-endemic fishes from the same lake are known to migrate there.

It has long been known (Trewavas, 1949) that these endemic lake species are often beautifully adapted to individual very definite environments within the lake. Such adaptations are very often reflected in the dentition, which in the various species is modified to various feeding habits. It seems that these and other specializations preclude the lake endemics from distributing themselves more widely. The question of their distribution into suitable micro-environments within their parent lake is in itself a problem which falls into the scope of the present paper, but time does not allow it to be further discussed.

The suitability of the environment is, of course, all-important. A special aspect of the question of ecological factors affecting the distribution of freshwater fishes is the case of the environment becoming, in the course of time, unsuitable for a particular species, which then dies out in the area affected by the change. Such cases are well known in general, but have been little studied in freshwater fish, amongst which our knowledge of taxonomy and ecology has mostly been insufficient to allow of work on this question.

One such problem is that of the distribution of the large-mouth "bream" *Serranochromis robustus* (Gunther) in the Zambezi system. The question here is that this well-known species occurs in suitable habitats in Lake Nyasa and the Upper Shire River, and was originally described from this area. But what is, in the present state of our taxonomic knowledge, considered to be the same species, any known differences being thought to be of subspecific importance at most, occurs again in the Upper Zambezi Okovango/Kafue area. It is not known from anywhere along the Zambezi River in between. This case of discontinuous distribution, where the Murchison Cataracts on the Shire River are separated from the Victoria

Falls on the Zambezi by a water distance of approximately 1,500 km., has puzzled taxonomists who found it difficult to recognize the same species from two such widely separated areas.

It is possible that this question may be resolved, at least in part, by considering some of the ecological factors involved. *S. robustus*, like all other members of the genus, has a distinct preference for water in which there is a good deal of aquatic vegetation: it is, in fact, a fish of those rivers for which I have in an earlier paper (Jackson, 1961a) proposed the term "reservoir" rivers. No case is known of a *Serranochromis* species inhabiting the other broad class of river, the "sand-bank" river of which the Middle Zambezi was, before the advent of Kariba, a typical example. Here the river, in contrast to the often marshy and always well-grown Upper Zambezi, dwindled to a comparative trickle between sand-banks during the dry season, with very little aquatic vegetation. Thus it is probable that the reason why *Serranochromis robustus* was absent from the long length of the Middle and Lower Zambezi was that conditions were ecologically unfavourable for it here during a large part of the year.

Now it is possible to postulate that this was not always so. It is possible that, at some past pluvial period, higher rainfall and reservoirs of water flowing into the Middle Zambezi made it more like the Upper Zambezi than it is now, so that *S. robustus* was able to inhabit the whole length of the river. When these favourable conditions came to an end, the fish was no longer able to exist in the middle and lower reaches, thus breaking the link between the populations in the Upper Zambezi and Upper Shiré. Weight may be added to this theory by the fact that, though the fish is absent from the Middle Zambezi River, occurrences of a *Serranochromis* have been reported from isolated parts of the Kalomo and Luansemfwa rivers, both of which flow into the Middle Zambezi. If such isolated populations do occur here, they may be remnants, which have survived in a favourable place, of a once much more extended population which at one time existed along the length of the Zambezi.

Worthington (1933) favoured also the view that communication between the Nyasan and neighbouring faunas took place along the Zambezi, but via the Kafue, which, after a tortuous course, enters the Middle Zambezi some 480 km. below the Victoria Falls. Here, again, past favourable conditions must have occurred to make the Middle and Lower Zambezi ecologically habitable for such species as *Serranochromis robustus* from this point down. An alternative theory, which can imply that *S. robustus* was never at any time in the middle and lower reaches of the Zambezi, is also mentioned by Worthington (*ibid.*, p. 288, footnote). This records that Captain C. R. S. Pitman had observed a definite channel of communication between the Rhodesian Congo and the Zambezi, between the upper reaches of the Luapula (Chambezi) and the Luangwa rivers. For *S. robustus*, the line of communication in this case would be from the Upper Zambezi Kafue through the Rhodesian Congo (where it is known) then into the Luangwa. From the Luangwa a similar process might have led to the fish entering the headwaters of some of the rivers which enter northern Lake Nyasa, such as the Songwe and the North Rukuru. Again, however, the ecological factor comes in, and it is necessary to postulate a more favourable environment in the past, because the Luangwa River to-day is one of the sand-bank rivers of Africa, and *S. robustus* is not known to occur in it.

The case of one species of fish has been put forward in some detail to illustrate the point that ecological preferences of a species must be understood in order to elucidate problems regarding its distribution. In general, ecological factors affect distribution in many ways. One factor very important in freshwater fishes is that of water temperature. Most tropical fishes are limited in distribution by being very sensitive to a temperature drop. Thus the widespread *Tilapia mossambica* Peters in its southward distribution becomes more and more limited to the lower altitudes nearer the sea until it is finally confined to river mouths and brackish lagoons along the north-eastern South African seaboard. On the other hand some species, such as the Mountain Catlet *Amphilius platycheir* Gunther, are even in the most

tropical parts of our region confined to cooler upland streams. Another factor is the need for cover, especially for smaller species which are more liable to predation by, e.g., the tiger-fish *Hydrocyon vittatus* Castelnau, than are those which reach a fairly large size when adult. In this regard Jackson (1961b) gives a table showing that the number of fish species known from the Middle Zambezi is very considerably less than those which are known from the adjacent Kafue and Upper Zambezi systems. Moreover, only 28.6 per cent of the Middle Zambezi fishes grow to a length less than about 18 cm. when adult, as against 55.5 per cent from the Upper Zambezi and 65.5 per cent from the Kafue, where there is better growth of aquatic vegetation all the year round.

The wide distribution of the top-minnows of the family Cyprinodontidae in tropical southern Africa can be explained by their small size and ability to colonize and live in the shallowest of waters, provided conditions of temperature are suitable and there is sufficient aquatic vegetation. One genus of the family, the brightly coloured *Nothobranchius* Peters, takes its adaptability to adverse physical conditions farther than most in that it is believed (Vanderplank, 1941) that eggs are laid which are drought-resistant, and can remain alive in the mud of a dried-up swamp until the advent of rain refills the swamp with water. It is clear that fish with this ability are well equipped to survive when other fish could not, a fact conducive to wide distribution.

I may finally stress that it is the eurytopic fish, able to tolerate a range of habitat, that is at once most likely to have a wide range of distribution and least likely to show any marked discontinuity. In general, the family Clariidae afford a wide range of examples and fields for further study. The genera and subgenera of this single family exhibit every phase, which is more or less accurately reflected in their distribution, from the widest ecological tolerance to the narrowest specialization. Much rests here on the development and use of the suprabranchial organ, which permits existence in foul or very muddy water. Species of the subgenus *Clarias* (*Heterobranchiodes*) have a wide and continuous distribution of the clinal type, so that it is extremely difficult to identify the species where the range of one species ends and that of the next begins. Thus *Clarias* (*H.*) *garipepinus* (Burchell) merges almost imperceptibly into *C.* (*H.*) *mossambicus* Peters, which again, further north, can scarcely be distinguished from *C.* (*H.*) *lazera* C. & V. where the ranges of the two overlap. The subgenus *Clarias* (*Clarias*) is considerably less catholic; the factor of temperature, among others, restricts its distribution, and only one species of this subgenus, *C.* (*C.*) *theodorae* Weber has a really wide distribution. The genus *Heterobranchius* Geoffroy is largely limited to large rivers and lakes, and there are other genera and subgenera, e.g. *Clariallubus* Boulenger, even more restricted.

One of the most remarkable of these groups are those restricted, and endemic to, lakes Nyasa and Tanganyika. A species-flock of endemic clariids is known from Lake Nyasa (Jackson, 1959), but only one from Lake Tanganyika. These behave in the same way as do other endemic forms in these lakes, being specialized to a narrow micro-environment and never being found even in affluent rivers where no large barriers exist. Greenwood (1961) shows that in these Rift Lake endemics the suprabranchial organs which are so strongly developed in the more eurytopic and widely distributed members of the family, are in all cases poorly developed and in some, entirely absent. From the point of view of distribution, however, the most remarkable of Greenwood's (*op. cit.*) findings is that, on morphological grounds alone, the single Tanganyikan species and the Nyasan species-flock are anatomically so alike that they should all be referred, in his opinion, to the single genus *Dinotopterus* Boulenger. This provides a most difficult problem in the field of animal distribution in southern Africa. How it is that of all the genera endemic to either one of these two widely separated lakes, this one alone has succeeded in colonizing both is a puzzle in distribution that no one yet has attempted to explain.

It is well to end on a note of puzzlement, because there are problems enough in the distribution of fish to make the field a stimulating one for the student of animal distribution. A single member of the genus *Bagrus* Cuvier, *B. meridionalis* Gunther, occurs in Lake Nyasa and the Upper Shire, but is absent from the Zambezi system, the Rhodesian Congo or Lake Tanganyika, the genus not otherwise occurring nearer than the large lakes and eastward-flowing rivers of East Africa. An endemic species-flock of the genus *Chrisichthys* Bleeker exists in Lake Tanganyika; there is only one, separate, species in the lakes and large rivers of the Rhodesian Congo and the genus is absent from any part of the Zambezi Kafue system or Lake Nyasa. Finally the distribution of the well-known electric catfish *Malapterurus electricus* Gmelin is markedly discontinuous in the area under review, for some reason as yet unknown. There is a belt, extensively watered, right across the sub-continent in which it does not occur. North of the belt it occurs in the Middle Congo and Lake Tanganyika. In the belt itself it is absent from the Upper Zambezi and Kafue, the Rhodesian Congo, including lakes Mweru and Bangweulu, and Nyasaland, including Lake Nyasa. Below the belt it reappears again in the Middle and Lower Zambezi and the Pungwe.

The above examples show that much remains to be discovered, but it nevertheless seems clear that it is not sufficient to take only physical characters of the environment into consideration. Important and indeed essential as these are, there are also ecological factors to be considered which may in some cases prove to be of as great importance. Environmental factors, such as for example a waterfall, may prove to be a barrier to a whole range of species belonging to several families, but ecological factors are more individual. The understanding of them necessitates research into the ecology of individual species; it may be, when such research has been done and the ecology of individual species better known, that the knowledge we have gained will contribute to a greater extent than we perhaps appreciate at present to our knowledge of the problems of animal distribution.

SUMMARY

Ecological factors are probably as important as environmental factors in governing the distribution of fish in tropical southern Africa. These factors are more individual in their effect on either restricting or extending distribution than are environmental factors. A waterfall may form a barrier to a large number of species, but a preference for weedy conditions may restrict only one of these. Examples are given of ecological tolerances operating both to extend the range or limit the distribution of various species. In an as yet unexplained case of discontinuous distribution along the Zambezi, it is postulated that changes in the environment put part of the area outside the range of ecological tolerance of the species concerned. Endemic lacustrine species, ecologically restricted to a narrow habitat, are less likely to have a wide distribution than are those species with a wider ecological tolerance.

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DISCUSSION

- Prof. Balinsky*: There is a need for sharper definition of the terms used in zoogeographical work. This paper, for instance, distinguishes between ecological factors and environmental factors, which most workers would regard as one and the same thing.
- Dr. Winterbottom*: Jackson states that the fish fauna of the upper Zambezi is much richer than the middle and lower reaches, but I would like to know how many species are common to both areas. The author classifies the middle and lower Zambezi as a "sandbank river", but the upper Zambezi is also a "sandbank river" in the dry season although, because it flows through flood plains, it has creeks and lagoons which provide additional and different environments.
- Dr. Talbot*: This is Mr. Jubb's work, but, as far as I remember it, there is an almost complete discontinuity between the upper and middle Zambezi.
- Mr. Atwell*: I do not altogether agree with Dr. Winterbottom regarding the upper Zambezi, which, I think, provides a much richer environment than the typical sandbank rivers.

R. S. CRASS

NATAL PARKS, GAME AND FISH
PRESERVATION BOARD.

Physical barriers and
the dispersion of freshwater
fish with particular reference
to Natal

A successful species extends its geographic range until a change in the environment prevents further dispersion. If the change is abrupt and clearly defined, such as that from dry land to water, it may be described as a physical barrier. An environmental transition of a more gradual nature, such as that associated with a decrease in temperature, forms a zone of ecological limitation. Physical barriers prevent animals reaching new territory whereas changing ecological factors make conditions unsuitable for the survival of species in areas that are accessible to individuals.

Barriers are of great importance zoogeographically, since isolation is a pre-requisite for faunal differentiation, but often an explanation for distributional patterns must be sought in the study of ecology. There is, indeed no fundamental distinction between physical barriers and ecological factors which limit dispersion. The sea is a physical barrier for terrestrial animals although its effectiveness varies according to an organism's structure and habits, and it is also a barrier for strictly freshwater fish. But if a fish has the necessary physiological adaptability it can move freely from fresh to salt water. While forming a definite physical barrier for some groups of organisms, the sea may have only an ecological influence on the distribution of others.

Faunistic changes which are correlated with local variations in topography and climate are of little or no significance to the zoogeographer. He is looking for broader patterns and relegates to the ecologist the task of correlating small scale variations in distribution with the mosaic of different habitats. Factors which are important ecologically may, however, be equally important zoogeographically.

Maximum and minimum temperature, for instance, vary from place to place within a limited area and often have a critical effect on the ecological balance. Latitudinal changes in temperature are highly significant to the zoogeographer, as shown by Poynton (1961) in relation to amphibian distribution in South Africa, and zonal temperature has undoubtedly played an important part in moulding the distribution patterns of many types of organisms.

It seems clear, therefore, that an ecological factor becomes zoogeographically significant if it limits or modifies patterns of distribution on an extensive scale. One of the main difficulties in utilizing factors such as temperature for the delimitation of zoogeographic regions, however, is to decide on a definite cartographical line of demarcation that corresponds with a significant change in the factor under consideration. No such difficulty occurs in discussing the effect of physical barriers, especially when dealing with a group such as freshwater fish

whose dispersion is curtailed by the sea, by divides between river systems and by waterfalls. The effect of these physical barriers is particularly noticeable on the eastern side of southern Africa between about 26° and 31° south latitude. Indeed the most remarkable point about the distribution of freshwater fish in that region is not that many species have failed to reach the more southerly rivers, but rather that some of them have overcome the barriers that lay in their path.

If a fish is to colonize new waters it must be able to swim there. Individual fish or fish eggs may possibly be transported by birds or by whirlwinds, but such factors are of negligible importance in the dispersion of a species. Human agency has played a part in the dispersion of certain fishes, but in general freshwater connections must be assumed to have existed wherever fish have spread from one body of fresh water to another. To reconcile this assumption with the observed discontinuity in the present habitats of many species requires the further assumption that past physiographic changes must have enabled fish to cross obstacles which are now impassable. The geomorphological history of a region provides clues to the nature of such physiographic changes.

No fossils of freshwater fish have been reported from south-east Africa, due perhaps to the recent origin of the fish fauna of Natal and the adjoining areas. Few endemic species occur and it appears probable that invasion of Natal rivers has taken place since the late Pliocene or early Pleistocene period when large scale tectonic movements occurred along the eastern edge of the African continent. In India a fauna which resembles that of south-eastern Africa in the absence of local specific differentiation is considered by Hora (1953) to have invaded its present habitat during the Pleistocene.

The criterion of taxonomic differentiation is, on its own, unreliable for estimating the age of a fauna since the rate of speciation may vary widely according to circumstances. Thus numerous endemic species of Cichlidae have evolved in Lake Victoria within a few hundred thousand years, whereas in other places species have remained unchanged for much longer periods. Brooks (1950) mentions the occurrence of two cyprinids, *Laheo weeksi* and *Barbus eutaenia*, in an affluent of Lake Tanganyika. He suggests that both species inhabited the river before the formation of the lake and that no differentiation has taken place in the comparatively stable environment despite isolation since the late Pliocene. The specific identity of populations isolated in different Natal river systems does not, therefore, given any accurate guide to their antiquity although it seems clear that such populations cannot be as old as those of the south-western Cape where each river system has its own endemic species.

Possibly the earliest freshwater fish to reach Natal rivers did so through capture of tributaries of the Orange River system by eastward flowing rivers. A large species of *Laheo* found only in the Tugela River is closely related to *Laheo capensis* of the Orange River system, and its origin appears to have been due to catchment exchange. Another endemic *Laheo*, which resembles the Orange River *L. umbratus*, presumably had a similar derivation. The dispersion of a very widespread minnow, *Barbus anoplus*, that occurs in many localities from the eastern Transvaal to the Gouritz and Olifants rivers in the Cape, may have been aided by catchment exchange. With the exception of these three species, however, there is no indication of any movement of fish from the interior plateau to Natal although a number of river captures took place in fairly recent geological times. One of the best known piracies was the diversion of the Slang River, which originally flowed into the Vaal-Orange system, but now forms the source of the Buffalo River and hence, part of the Tugela system. The capture of the Slang took place during the Pliocene period and should have resulted in a transfer of fish species from the Orange to the Tugela had the fish been present at the time of capture. In fact, however, the Slang contains only *Barbus anoplus*. The characteristic Orange River forms are all absent from the Slang and the large *Barbus* and *Laheo* of the Tugela have been denied access by waterfalls.

The significance of waterfalls in limiting dispersion will be considered later, but first we must attempt to explain how the bulk of the fish fauna reached the waters in which they occur today. There is no difficulty in understanding how fish have moved from the Zambezi southwards to the Usutu-Pongolo system. Apart from the possibility that the Zambezi may at one time have flowed southwards to enter Delagoa Bay, sporadic flooding of the Mozambique plain could have enabled fish to swim from one river to another. The occurrence of many Zambezi species as far south as the Pongolo gives support to the assumption that a migration route has at times been available.

Seventeen of the Pongolo species are, however, absent from the rivers that flow across the Zululand coast plain and another four of the Pongolo species fail to reach the Tugela River, although low-lying land near the sea seems to offer the possibility of intermittent connection between different rivers. South of the Tugela the rivers are deeply entrenched in a terrain of high relief and debouch onto a narrow strip of low-lying coast before entering the sea. The number of species decreases southwards, but a few fishes are found in all Natal rivers. Beyond the Natal-Cape border the Umzimvubu River system is populated only by *Barbus anoplus*, a species which has a remarkably wide distribution from the Incomati River system in the northeast to the Gouritz River in the southwest.

The majority of Natal species whose range extends into the Province from farther north probably moved from river to river along the coast. Exchange of tributary streams between neighbouring river systems may have had some effect in aiding the movement of fish from one system to another. Tributary streams entering a river from the north have steeper courses, in general, than those entering from the south and might, therefore, incise more rapidly and so capture a neighbouring stream flowing in the opposite direction. The reason for the steeper gradient of northern tributaries is that the north side of an east flowing river valley is usually steeper than the south side, due to the effect of aspect on the rate of erosion. There is no evidence, however, that catchment exchange between Natal river systems has played a part in the dispersion of fish.

There is no conclusive evidence of any freshwater connections between Natal rivers, but there is a reasonable probability that such connections did exist at times through lagoons close to the sea. At the present time rivers tend to form lagoons behind the sand dunes that run parallel with the beach along the Natal coast. Each river tends to have its own lagoon, separate from those of its neighbours, but coastal dunes are subject to considerable variation, and the formation of a long continuous dune that temporarily blocked the mouths of several neighbouring rivers might create a body of fresh or slightly saline water connecting the different rivers. Within historical times the Umgeni, Umlaas, Isipingo and Umbogintwini rivers all flowed into Durban Bay. Very considerable fluctuations in the relative levels of land and sea occurred during the Pleistocene period and at certain stages the damming up of river mouths behind coastal dunes, built up by the sea, might have brought about the coalescence of individual lagoons.

The likelihood that fish reached Natal rivers along the coast is borne out by the occurrence of such dominant species as *Barbus natalensis* in the lower reaches of all the rivers, as far south as the Umtamvuna. They are found upstream towards the headwaters, except where waterfalls have prevented the ascent of a river. But now we find a very interesting phenomenon: certain waterfalls have had no apparent effect on dispersion whereas others have formed an insurmountable barrier.

The explanation for this anomaly is to be found in the geomorphological history of the region. King and King (1959) postulate a mighty upwarping that raised the land along an axis parallel to and not far from the Drakensberg escarpment. This large scale movement took place at the end of the Pliocene or early in the Pleistocene and resulted in a steepening of the courses of all the Natal Rivers. The increased gradient caused accelerated erosion and the

formation of the deeply incised valleys so characteristic of the landscape as we see it today. As the rivers cut downwards they encountered some rock formations that were harder than others. Dolerite is particularly resistant and wherever a sill or dyke of this rock crossed the course of a stream a waterfall developed. At the present day such falls may be of very considerable height; the Howick Falls, for example, on the Umgeni River are 311 ft. high. Yet these and other similar falls in the Natal midlands have not prevented *Barbus natalensis* from reaching sections of river farther upstream. The only reasonable conclusion is that the falls were not sufficiently well developed at the time of invasion of the rivers to form a barrier to upstream movement of the fish. Too many falls are involved to explain the presence of fish upstream by suggesting that transfer was effected by human or other adventitious agency.

Falls that occur at over 4,000 ft. altitude, towards the foot of the Drakensberg, have, in contrast to those lower down, acted as complete barriers to upstream movement of fish. This applies even on rivers where a considerable length of water suitable for *Barbus natalensis* occurs above the falls. Another point is that some of these barrier falls are not more than 15 or 20 ft. high. They are, however, situated above those sections of river which were affected by the Pleistocene steepening of the gradient. They have therefore presumably been in existence considerably longer than the far more impressive falls at lower elevations. Their greater age would account for their more significant effect as barriers to the dispersion of fish. In other parts of Africa the importance of waterfalls is well known. To mention only a few, the Semliki Falls, the Murchison Falls, the Murchison Rapids on the Shire and the Chibirira Falls on the Sabi have all had a marked influence on fish distribution by preventing access to the rivers above the falls.

The time of colonization of Natal rivers by *Barbus natalensis* and other widespread species was most probably early in the Pleistocene, when tectonic movements may have produced a temporary route along the coast, and before the waterfalls that interrupt the lower and middle courses of the rivers today had become established. The fact that many species which occur on Natal's northern border have not reached the more southerly rivers is easily explained if they are considered as representatives of later waves of migration. That explanation may not, of course, always be the correct one. Ecological requirements may enter the picture and also some species have better powers of dispersion than others.

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DISCUSSION

Mr. Stuckenberg: With regard to waterfalls as barriers, I am not altogether satisfied about the large Pliocene uplift postulated by King. Other authors are generally agreed that there were at least three major uplifts during the Tertiary. The effects of this particular uplift and the dating of Natal fish populations do not seem to my mind to be well established.

Prof. Balinsky: I have an uneasy feeling that the picture presented here is incomplete. It is taken for granted that most or all of these fish have migrated from thousands of miles away; but surely there were fish in Natal earlier than the Pleistocene. They are an old group. Unless there is some reason for thinking that there were no fish earlier than this period or that conditions in the region were untenable for fish, we must look upon this presentation with some doubt as the rivers are also very old.

F. L. FARQUHARSON

DEPARTMENT OF NATURE
CONSERVATION, TRANSVAAL
PROVINCIAL ADMINISTRATION
WRITTEN WHILE AN OFFICER OF THE
NATAL PARKS, GAME AND FISH
PRESERVATION BOARD.

The distribution of cyprinids in South Africa

The most characteristic feature of the freshwater fishes in Southern Africa is the surprising reduction in the number of families represented in central and eastern Africa. The dominant family in southern Africa is the Cyprinidae. This family is represented by the genera *Labeo*, *Varicorhinus*, *Barbus*, *Barilius* and *Engraulicypris*, none of which is endemic to the region. Of these genera, *Varicorhinus* is of doubtful status while *Barilius* and *Engraulicypris* are probably each represented by single species.

In southern Africa, some groups of the Cyprinidae show a surprising degree of endemism whereas other groups have a very widespread distribution. This paper is an attempt to group the various Cyprinids of the region, to give a general account of their distribution and to give possible explanations to the problems posed by such distribution.

ACKNOWLEDGEMENTS

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I am indebted to the Director of the Natal Parks, Game and Fish Preservation Board, Col. J. Vincent, for the facilities provided while employed in his Department, to the Officers of that Board who assisted in the collection of material, to Mr. R. A. Jubb for valuable information on the distribution of various species, to Professor S. F. Bush and other members of the University of Natal who have supplied valuable information, and to the Directors and Staff of the South African and Natal Museums for making available material and records.

In this paper taxonomically related species have been aggregated into provisional groups (A to L) and are listed below. As the synonymy of the various species is extremely involved, the respective synonyms have not been listed with the species cited.

GROUP A *Labeo* in which the inner surface of the lips do not bear transverse plicae.

					Lateral line	Caudal peduncle
					Scales	Scales
<i>L. altivelis</i>	36-39	16-18
<i>L. rosae</i>	37-40	18-20
<i>L. tenuirostris</i>	40-42	18-20
<i>L. rubromaculatus</i>	41-45	20-24
<i>L. capensis</i>	47-50	20-24
<i>L. umbratus</i>	57-65	30-34
<i>L. quathlambae</i>	65-68	30-34
? <i>L. seeberi</i>	82-90	36-50

GROUP B	<i>Labeo</i> which do bear transverse plicae on the lips.					
	<i>L. forskalii</i>	37-42	16-20
	<i>L. congoro</i>	38-40	16-18
	<i>L. cylindricus</i>	38-39	18-20
	<i>L. darlingi</i>	36-39	16-20
	<i>L. rubropunctatus</i>	36-39	18-20
GROUP C	<i>Barbus</i> in which the scales are small and longitudinally striated.					
	<i>B. natalensis</i>	33-34	16-18
	<i>B. holubi</i>	38-41	16
	<i>B. kimberleyensis</i>	37-45	16
	<i>B. capensis</i>	41-45	16-18
GROUP D	<i>Barbus</i> (and <i>Varicorhinus</i>) in which the scales are large and longitudinally striated.					
	<i>B. marequensis</i>	27-34	12-14
	<i>V. nelspruitensis</i>	36-40	14
	<i>V. pungweensis</i>	28-30	12
GROUP E	<i>Barbus</i> in which the scales are radiately striated, possessing a serrated dorsal spine and in which the adults attain at least 20 cms. standard length.					
	<i>B. mattozi</i>	33	14
	<i>B. rapax</i>	29-35	14
	<i>B. andrewi</i>	38-40	16
	<i>B. serra</i>	41-44	20
GROUP F	<i>Barbus</i> in which the scales are small and radiately striated, possessing a serrated dorsal spine and in which adults seldom attain more than 10 cms. standard length.					
	<i>B. paludinosus</i>	32-36	16-18
	<i>B. hospes</i>	37-39	16
	<i>B. calidus</i>	34-38	14
	<i>B. trevelyani</i>	33-36	14
	<i>B. ivongoensis</i>	34	14
	<i>B. afrohamiltoni</i>	29-34	16
	<i>B. argenteus</i>	27-33	14
GROUP G	<i>Barbus</i> in which the scales are large and radiately striated, possessing a serrated dorsal spine, and adults seldom attaining more than 10 cms. standard length.					
	<i>B. eutaenia</i>	24-27	12-14
	<i>B. multilineatus</i>	25-27	10-12
	<i>B. afrovernayi</i>	27-29	12
	<i>B. kessleri</i>	24-26	12
	<i>B. tangandensis</i>	22-24	12
GROUP H	<i>Barbus</i> in which the scales are radiately striated and in which the dorsal spine is not serrated.					
	<i>B. trimaculatus</i>	30-35	14-16
	<i>B. bernardcarpi</i>	31-35	14

THE DISTRIBUTION OF CYPRINIDS IN SOUTH AFRICA

GROUP I <i>Barbus</i> in which the scales are small and radiately striated, and a true dorsal spine is lacking.					
<i>B. senticeps</i>	30-34	12
<i>B. burchelli</i>	28-36	12
<i>B. phlegethon</i>	30-36	12
<i>B. tenuis</i>	32-36	12-14
<i>B. vulneratus</i>	33-36	12-14
<i>B. asper</i>	34-38	14-18
<i>B. anoplus</i>	32-36	14-16
<i>B. labialis</i>	33-37	16
<i>B. gurneyi</i>	31-35	12-14
<i>B. inermoides</i>	35	12
GROUP J <i>Barbus</i> in which the scales are large and radiately striated, and a true dorsal spine is lacking.					
<i>B. viviparus</i>	28-31	12
<i>B. thamalakanensis</i>	25-28	12
<i>B. lineomaculatus</i>	27-32	12
<i>B. puellus</i>	27	12
<i>B. rubellus</i>	24-26	12
<i>B. treurensis</i>	26-30	12
<i>B. barotseensis</i>	26-29	12
<i>B. radiatus</i>	26-27	12
<i>B. toppini</i>	27-28	12
<i>B. pallidus</i>	27-30	12
<i>B. annectens</i>	27-29	12
<i>B. barilioides</i>	28-30	12
<i>B. fasciolatus</i>	25	12
<i>B. palustris</i>	26-28	12
<i>B. aurantiacus</i>	26-28	12
GROUP K <i>Barilius</i> species.					
Only one species in the area.					
<i>B. zambesensis</i>					
GROUP L <i>Engraulicypris</i> species.					
<i>E. brevianalis</i> , <i>E. gariepinus</i> and <i>E. whitei</i> .					

DISTRIBUTION

Genus *Labeo*: Groups A and B.

There are at present 13 recognised species in southern Africa.

GROUP A (Fig. 1)

Of this group, *L. capensis* and *L. umbratus* share the Orange System, but the latter, possibly through catchment exchange, has gained access to the southern Cape watershed. A species closely related to *L. capensis* is *L. rubromaculatus*, found only in the Tugela System. *L. quathlambae*, apparently related to *L. umbratus*, is found in the upper Umkomazana River. Both these Natal fishes undoubtedly gained access to their respective localities through catchment exchange high in the Drakensberg. The Limpopo System has two

species of this group, *L. tenuirostris* and *L. rosae*, of which the latter extends southward to the Pongolo River. To the North, the group is represented by *L. altivelis*, from the Zambezi to the Sabi-Lundi Rivers. *L. seeberi* from the Olifants River of the South Western Cape has been assigned to this group following information from Mr. R. A. Jubb (unpublished).

The general picture of this group is an almost continuous distribution from the Zambezi to the Cape. The degree of speciation and the southern limits of this group suggest a relatively old dispersion.

GROUP B (Fig. 2)

In this group *L. cylindricus*, *L. darlingi*, *L. congoro* and *L. forskalii* are found in the Zambezi, however the latter apparently replaces the former above the Victoria Falls. *L. cylindricus* extends southward to the Pongolo River while *L. darlingi* extends a little farther south to the Tugela River. *L. rubropunctatus* is the only species of this group not found in

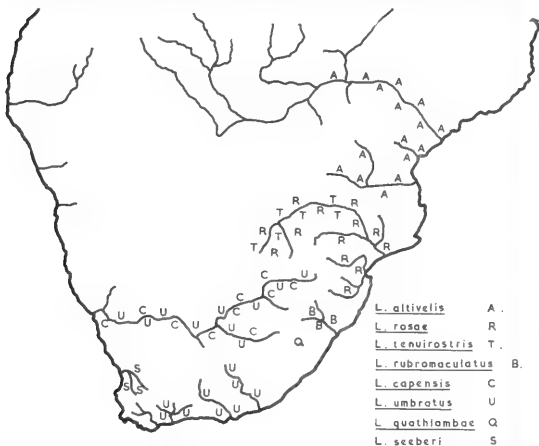


Figure 1. Group A.

the Zambezi and its distribution is from the Limpopo southward to the Pongolo River.

This group is probably of a more recent dispersion than group A as, apart from a smaller degree of speciation and endemism, it has not extended as far southward.

Genus *Varicorhinus*. The Southern African representatives of this genus closely resemble species of the genus *Barbus* and the only character separating these genera is qualitative. Unfortunately this problem of systematics cannot be dealt with here so for the purposes of this paper the two species of *Varicorhinus* are listed as distinct species in group D.

Genus *Barbus*: Groups C to J inclusive.

Forty-eight species of this genus have been listed in this paper but as there is still some taxonomic confusion in this genus it is likely that a number of these species will become synonyms in the future.

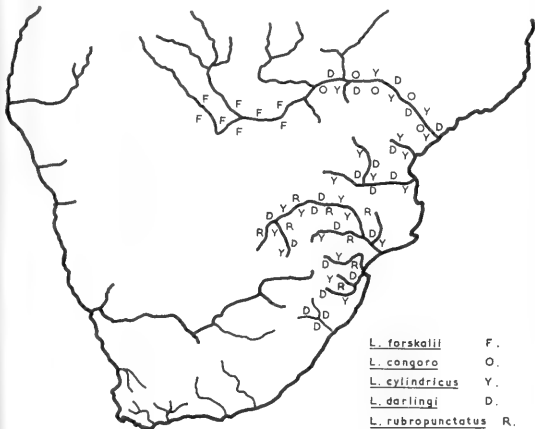


Figure 2. Group B.

GROUP C (Fig. 3)

B. natalensis occurs in the Limpopo and all East-flowing rivers southward to the Umtamvuna. Two species, *B. kimberleyensis* and *B. holubi* are endemic to the Vaal-Orange System. *B. capensis* is endemic to the Olifants River of the South Western Cape.

Although this group appears to be absent from North of the Limpopo River to the Zambezi, it is represented in Central Africa and elsewhere. The endemism and widespread distribution probably indicates an old dispersion possibly contemporaneous with that of group A.

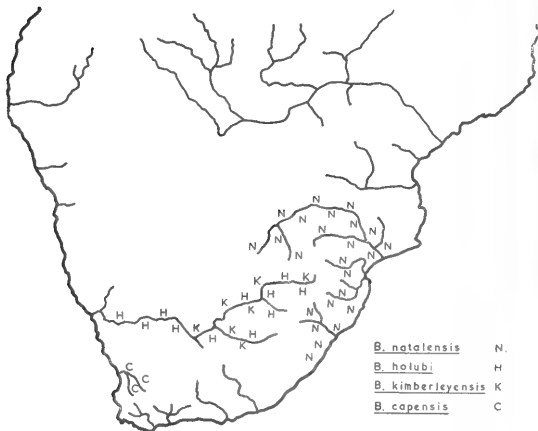


Figure 3. Group C.

GROUP D (Fig. 4)

B. marequensis is found in all East-flowing rivers from the Zambezi to the Pongolo. *V. pungweensis* is found, as the name suggests, in the Pungwe River and *V. nelspruitensis* occurs in the Incomati and Pongolo-Usutu Systems.

As no members of this group are to be found in the Orange System or South of the Pongolo River, it is suggested that the dispersion of this group is fairly recent, possibly occurring at the same time as that of group B.



Figure 4. Group D.

GROUP E (Fig. 5)

B. mattozi occurs in the upper reaches of the Zambezi System. *B. rapax* is found in certain sections of the Limpopo and its tributaries. *B. andrewi* and *B. serra* are found in the South-western Cape area, the former in the Berg and Breede Rivers and the latter in the Olifants River.

Apart from the geographic isolation of the members of this group, it is interesting to note that there are no records of the group between the Zambezi and North Africa where it is again represented. The dispersion of this group probably dates to that of group A and C or perhaps even earlier.

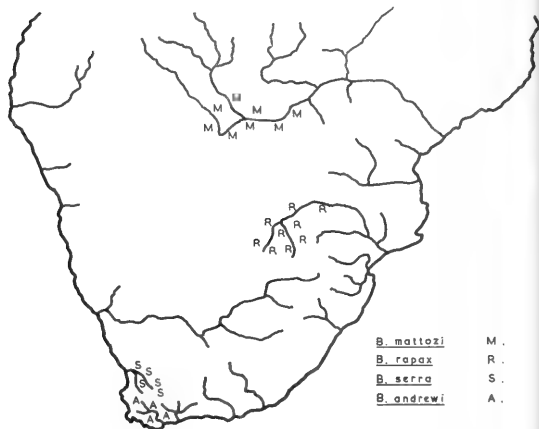


Figure 5. Group E.

GROUP F (Fig. 6)

The distribution of this group is particularly interesting as it seems to indicate two separate phases of dispersion. The earlier dispersion gave rise to a number of endemic species at more or less isolated localities in southern Africa. *B. hospes* is endemic to the lower Orange River and *B. callidus* to the Olifants River. On the east coast, *B. trevelyani* is to be found in a few rivers around the King William's Town area, *B. ivongoensis* in the Ivongo River (Natal South Coast) and *B. afrohamiltoni* is found from the Pongolo to the Sabi-Lundi System. *B. argenteus* is known from the Incomati and Pongolo Rivers but has also been recorded from the Kunene River. The second or later phase of dispersion brought about the widespread distribution of *B. paludinosus*, from the Zambezi and Pongolo Rivers in the north of the region to the Orange on the west coast and the Umhloti River (Natal) on the east coast.

The earlier phase of dispersion may have occurred along with those of groups A, C and E, while the later phase probably dates with those of groups B and D.

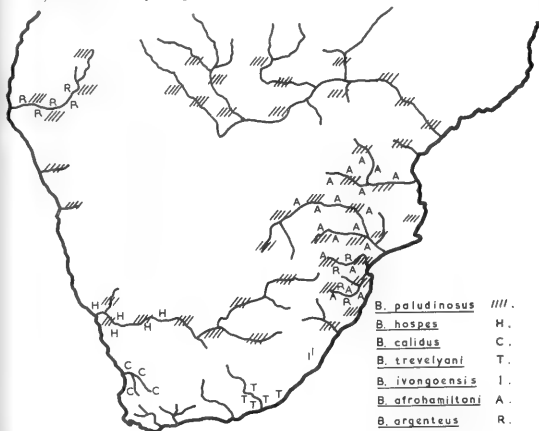


Figure 6. Group F.

GROUP G (Fig. 7)

B. eutaenia is found from the Zambezi and Kunene Rivers southward to the Limpopo River. This species may be synonymous with *B. kerstenii* from East Africa. *B. tangandensis* is found in the upper Zambezi, *B. multilineatus* and *B. afrovernayi* in the middle Zambezi, but the latter has also been recorded from the Kunene River. *B. kessleri* is found around the Beira area.

It may be that this group also shows two phases of dispersion with *B. eutaenia* representing the widespread form and regarding the other species as relicts, but further information is required on this group. Assuming two phases to have occurred, the tentative dating would be similar to that of group F.



Figure 7. Group G.

THE DISTRIBUTION OF CYPRINIDS IN SOUTH AFRICA

GROUP H (Fig. 8)

This group is represented in the area by only two species, *B. bernardcarpi* in the upper Zambezi and Okovango areas and *B. trimaculatus* from the Zambezi and Kunene Rivers southward to the Tugela River in the east and to the Vaal River but apparently not the Orange River in the west.

The dispersion of this group occurred probably at the same time as that of groups B and D.



Figure 8. Group H.

GROUP I (Fig. 9)

This group, like group F, is characterised by having a widely distributed species, *B. anoplus* and a large number of very localized species. *B. anoplus* is found probably from the Incomati system southward to the Great Fish River of the eastern Cape and also in the Orange-Vaal System. It appears to have gained access from the latter to the Gouritz System and the Olifants River. *B. senticeps* is found in the Zwartkops and Kromme Rivers, *B. tenuis* in the Gouritz River, *B. burchelli* in the Berg and Eerste Rivers, *B. phlegethon* in the Olifants River, *B. vulneratus* in the Breede River, *B. asper* in the Gouritz to the Gamtoos River, *B. labialis* in the Limpopo System, *B. inermoides* in the Kunene River, and *B. gurneyi* from the Umtamvuna River northwards to the Incomati System.

It seems likely that this is another group with two phases of dispersion, the earlier phase probably occurring along with that of group E, but it is difficult to date with any degree of

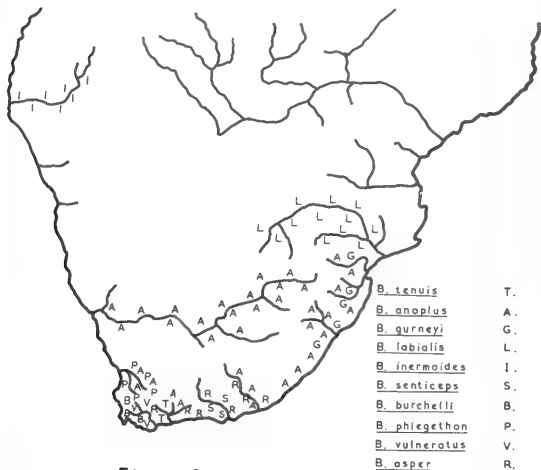


Figure 9. Group I.

THE DISTRIBUTION OF CYPRINIDS IN SOUTH AFRICA

accuracy the dispersion of *B. anoplus* owing to the fact that the group is apparently not represented in the Zambezi System nor in the rivers southward to the Limpopo, and also because of the fact of its presence in the Olifants River of the south-western Cape.

GROUP J (Fig. 10)

Due to the synonymy, the apparent randomness of distribution and the confusion of names, individual species localities will not be cited, but reference should be made to figure 10.

As a whole the group extends from about Port Elizabeth northwards to beyond the Zambezi System and is also represented in the Vaal and Kunene Rivers and in the Okavango area. Little can be said about the dispersal of this group until the systematics are further worked out and more precise data is available. It is however probably yet another group showing a twofold dispersion with *B. viviparus* as the widespread species.

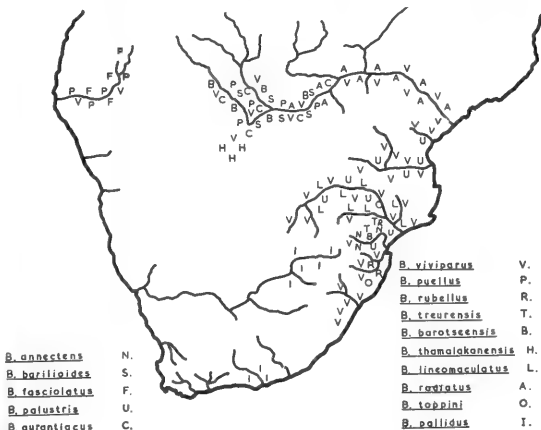


Figure 10. Group J.

Genus *Barilius*

GROUP K (Fig. 11)

The genus *Barilius* is represented in Southern Africa by probably only a single species, *B. zambesensis*. The distribution of this species extends from the Zambezi southwards to the Pongolo River. Its dispersion probably occurred about the same time as that of groups B and D.

Genus *Engraulicypris*

GROUP L (Fig. 11)

Three species of this genus have been recorded from Southern Africa; *E. brevianalis* from the Dwaars River (Transvaal) and from the Pongolo to the Umfolozi Rivers in Natal; *E. whitei* from the Limpopo System; and *E. gariepinus* from the Orange River. All three species are highly variable and it seems probable that only one or perhaps two species will be recognised in the region when material from sufficient localities is compared.



Figure 11. Groups K & L.

THE DISTRIBUTION OF CYPRINIDS IN SOUTH AFRICA

DISCUSSION

The Influence of Water Temperature on Scale Formation

Barnard makes reference to Mottley (*Fishing Gazette* cxv, No. 3155, Oct. 1937) who found that the number of scales in North American trout is dependent on the temperature at the eyed-egg stage and for about five weeks thereafter: the higher the temperature the lower the scale-count. Although water temperature data are not available as yet, it is interesting to note the variation in scale count in groups A and E when the species are arranged in order of localities—approximately from "hot" to "cold".

TABLE I

GROUP A

Species	Locality	Lateral Line Scales
<i>L. altivelis</i>	Zambezi	36-39
<i>L. rosae</i>	Limpopo—Pongolo	38-40
<i>L. tenuirostris</i>	Upper Limpopo	40-42
<i>L. rubromaculatus</i>	Tugela	41-45
<i>L. capensis</i>	Orange	47-50
<i>L. umbratus</i>	Orange and S. Cape	57-65
<i>L. quathlambae</i>	Upper Umkomazana	65-68
<i>L. seeberi</i>	Olifants	82-90

GROUP E

Species	Locality	Lateral Line Scales
<i>B. mattozi</i>	Zambezi	33
<i>B. rapax</i>	Limpopo	29-35
<i>B. andrewi</i>	Berg and Breede	38-40
<i>B. serra</i>	Olifants	41-44

Although practically nothing is known of the breeding habits of these species, it seems probable that these figures are a further corroboration of Mottley's findings. I do not suggest that the species within the two groups are synonymous but only that they share recent common ancestry.

Apparently converse to the above findings, *Barbus natalensis* shows a reverse correlation of scale-count to water temperatures. Table 2 gives the average lateral line scale counts of this species from Natal and the Transvaal in a north to south sequence.

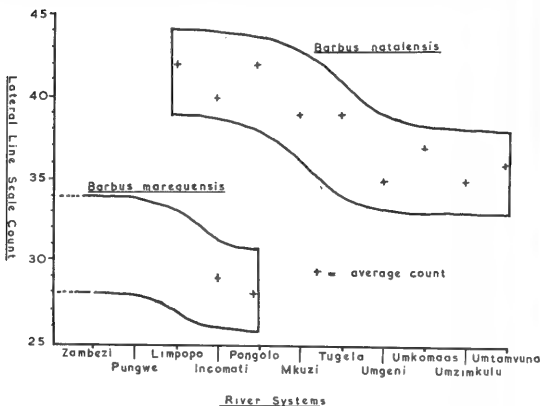
TABLE 2

Lateral Line Scale-counts in *Barbus natalensis*

River	Lateral Line Count
Limpopo (Marico River)	42 average
Incomati (Komati River)	40 "
Pongolo-Usutu (Usutu River)	42 "
Mkuzi River	39 "
Tugela River	39 "
Umgini River	35 "
Umkomaas River	37 "
Umkimkulu River	35 "
Umtamvuna River	36 "

The picture in Table 2 is however complicated by the fact that the southern limit of distribution of *Barbus marequensis* occurs almost in the middle of the range of *B. natalensis*. Thus if the scale counts of the one species are plotted with those of the other as in Table 3, the correlation with water-temperature becomes less significant.

TABLE 3



Lateral Line Scale-Count

My interpretation of this north/south variation in scale-counts lies in the theory of divergence of species.

Assuming that *Barbus natalensis* occurred in its present distribution originally with a range in the lateral line scale count of from 35 to 39, and that *B. marequensis* was a later invader with a count of from 28 to 34, the theory of divergence of species would suggest that where the two species occurred together a divergence of characters common to both would take place in time.

The evidence in Table 3, I believe, supports the above assumptions and hypothesis but further work on other characters will have to be undertaken before confirmation.

Dispersal

Cyprinids are known as Eocene fossils in Europe and as Miocene fossils in North America but no references to Tertiary fossil Cyprinids could be found from southern Africa.

As this family is found exclusively in fresh water (classified by Myers as a First Order fresh-water fishes), how did they get to their present localities?

Various hypotheses have been put forward to explain this question - the most important of these being:

- (1) Transport of young fish or eggs on the legs of birds, e.g. ducks and waders;
- (2) Exchange of river catchments;
- (3) Reversal of flow in rivers by continental tilting;
- (4) Pluvial periods;
- (5) Submergence and emergence of coastlines.

Of the above hypotheses, (1) is of minor importance unless the two river systems were in close proximity and if so it is more probable that (2) would account for the dispersion. It is however unlikely that (2) could account for the colonization of the whole of southern Africa. There appears to be little evidence for (3) in southern Africa. Pluvial periods and rise and fall of the coastline are discussed in more detail below.

Pluvial Periods and Geological Evidence

Although Pluvials are known to have occurred in Central and East Africa there appears to be little evidence for such occurrences in southern Africa. Kokot (1948) maintains that since the Pleistocene there has been a dry Kalahari Period followed by the return of more humid conditions, and he discounts any idea of pluvials during the latter period in this region: "... at no stage was the rainfall much more than it is now for any great length of time". Against this, Janmart has found in Angola three separate stages of Kalahari Sands interspersed with fluvial deposits dating from the Middle and Upper Pleistocene. At the Victoria Falls, Clark has demonstrated a series of Kalahari-type Sands alternating with fluvial deposits of the same date, and similar deposits have also been found on the Vaal River.

Cooke (1959) is of the opinion that the stratification mentioned above indicates very dry intervals rather than very wet periods, and that author, working on the structure of the sand particles also dates these periods as Middle and Late Pleistocene.

Thus according to the geologists the Early Pleistocene was an extremely dry phase followed by a return to conditions not unlike the present, but interspersed with further dry periods. Such fluctuations in conditions would undoubtedly result in considerable erosion and so the hypothesis of catchment exchange as a means of dispersal becomes more significant.

Submergence and Emergence of Coastlines

According to Barnard, the Breede, Gouritz and Gamtoos Rivers each have their own characteristic fish fauna and also contain the remnants of Cretaceous beds. As the genus *Barbus* is not known from pre-Tertiary times, the fish must have entered well after the establishment of these rivers.

Du Toit and Krige consider the extended Breede to have joined the extended Gouritz before the resubmergence of the Agulhas Bank in the Late Pleistocene, but according to Barnard the fish faunas of the two rivers are totally different. Hence these rivers must either have been populated before the Late Pleistocene and become differentiated since then, or they were never joined. Barnard regards the latter conclusion as the more plausible.

The rise and fall of the eastern coastline of Africa could account for the southerly dispersion of many species. There is little doubt that the Limpopo, Incomati and Pongolo-

Usutu Systems were joined in the past and they may also have been joined by a southerly extension of the Zambezi.

From the Tugela River northward to the Zambezi there is an ever widening low lying coastal plain considerable portions of which become inundated in the rainy season giving fish access from one area to another. Through Natal and Pondoland the coastal shelf becomes very narrow and the coastline steeper, making access from one river to another increasingly difficult—in fact there is only one Cyprinid, *Barbus anoplus*, whose distribution range extends southward through the rivers of Pondoland into the Cape proper. Another curious feature of this fish is that it is the only species that is present in the Olifants River (S. W. Cape) that is not endemic to that river.

I have suggested earlier in this paper that there have been two or more "waves" of Cyprinid dispersal in Southern Africa. The wet and dry periods during the Pleistocene were a somewhat cyclic occurrence as also appears to be the rise and fall of the coastline. These in themselves would suggest alternating periods whereby the fishes could move from one area to another. The evidence from the distribution patterns of the various groups, and in some the combination of "relict" endemics and a single wide-spread species, further confirms this.

That there have been two Cyprinid "invasions" during the Pleistocene seems probable, but the existence of present species prior to that time is uncertain. The fishes of the Olifants River (S. W. Cape) Cyprinids and other families represented, suggest perhaps an earlier origin.

CONCLUSIONS

Southern Africa has been subject to a series of Cyprinid invasions. The remnants of the earlier invasions have become isolated in the various river systems and have undergone speciation to a greater or lesser extent. Later invaders have ousted some of their predecessors in many systems thus giving the relict fauna its characteristic discontinuous distribution.

There appears to be nothing in southern African rivers which could account for their not being colonized by Cyprinids. The only factor preventing such distribution appears to be the accessibility of rivers to the fish.

Rise and fall of the coastline and exchange of river catchments during the Pleistocene appear to be the main factors in dispersal. Factors accounting for dispersal, occurring in a cyclic manner, have given rise to a wave form of dispersion.

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DISCUSSION

Dr. Macnae: Except at the Zambezi mouth, the continental shelf of the east coast of southern Africa is rather narrow, varying from about two to five miles in extent. I suggest, that this is insufficient to support the idea that a rising and falling coastline can have afforded much aid to distribution.

Mr. Farquharson: The coastline is steepest in the Pondoland area and it is interesting that that region has only one species.

- Dr. Talbot:* Although it seems fairly reasonable to assume that there may have been a series of two or more Cyprinid invasions in southern Africa, I think that the patterns of distribution here described could also arise in other ways. The existence of a single widespread species in several of the groups is not really proof of "wave" invasion.
- Dr. Winterbottom:* I am not sure whether Dr. Talbot is right. In the presence of a single widespread species, it is difficult to know how other species could develop unless they all arrived in the area in a series of different waves.
- Prof. Ewer:* Lack has emphasized Gause's principle which states that when two closely related species occupy the same habitat they must be ecologically differentiated if one is not to eliminate the other through competition. This seems to support Dr. Talbot.
- Dr. Winterbottom:* I think this raises an entirely different question. Is there any evidence of ecological isolation between the clusters of related species which occur in the lakes?
- Mr. Farquharson:* All the endemic species are physically isolated, each being peculiar to an isolated river system. In the lakes, differences in breeding behaviour appear to be the main isolating factors.
- Mr. Grindley:* In the Cape we appear to have a relict of a paleogenic fauna in *Galaxias*.
- Mr. Farquharson:* These fish, rather like trout, are probably of marine origin and there is no good evidence that they are paleogenic.
- Dr. McLachlan:* Have the Cyprinids any tolerance of salinity? I ask because there is often seepage into the areas behind coastal dunes forming pools and lagoons which may be more or less salty or fresh. These may afford a pathway between river systems.
- Dr. Stuckenberg:* I have investigated some of the insects inhabiting such pools, and have found them all widespread, unspecialized forms.
- Mr. Farquharson:* Salt tolerance in Cyprinids is probably low.
- Prof. Ewer:* Do you base this on observations or experimental measurements?
- Mr. Farquharson:* On the observation that they do not occur near estuaries.
- Mr. Liversidge:* *Barbus* does occur in the lower more saline reaches of the Olifants River, but it is rare.
- Dr. Harrison:* We found *Barbus* in the estuary of the Olifants River only after floods which had pushed the salt water right out of the lagoon.
- Prof. Ewer:* Here again we must distinguish between habitual selection and tolerance. The point is that although the fish might not generally choose to live in saline estuaries they could use these conditions to move from one river to another.
- Mr. Liversidge:* During floods in the eastern Cape, fresh water from the Sundays River actually flowed along the coast to well beyond the Bushmans River mouth. It is thus conceivable that fish might get from one to the other with only a small degree of salt tolerance.
- Dr. Harrison:* This is a very good point and worth further investigation. At False Bay, St. Lucia for instance, we found many skulls of *Clarias* which had apparently come down river and died, but we found no remains of *Barbus*.

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Patterns in the distribution
of the
Southern African amphibia

The ranges of the various forms of amphibians in southern Africa conform to a few very distinctive basic patterns. The distribution of the southern African Amphibia has already been outlined in a general way (Poynton, 1960), and the aim of this paper is to show selected examples of the different types of patterns. It is not proposed to give here a close analysis of the factors which might be responsible for imposing common patterns on different amphibian forms. The profound differences in the ecology of different amphibians in southern Africa should, however, be emphasized in order to discourage any simple explanation of the determination of amphibian distribution patterns. For example, species of *Xenopus* Wagler are almost totally aquatic, whereas species of *Breviceps* Merrem and *Arthroleptis* Smith pass the entire life cycle away from water. The fact that animals of such diverse ecology as the Amphibia conform to the same general patterning indicates that one must look for causal factors beyond features such as water and soil composition, and even vegetation, to the fundamental background of the prevailing temperature and rainfall. The complexity of the situation is further shown by there being not one but six different basic patterns shown by the Amphibia in southern Africa. Examples of each type of pattern are here presented with the intention of inviting comparisons from workers on the distribution of other groups, since the more general these patterns turn out to be, the easier should be the task of explaining them.

The Tropical Pattern. No tropical form covers the whole of southern Africa. The ranges of two of the most widespread tropical forms, *Phrynobatrachus natalensis* (Smith) and *Kassina senegalensis* (Duméril and Bibron), are shown in Figs. 1 and 2 respectively. Neither of these occur in the south-western Cape, a feature common to all tropical forms. These forms are also absent from the arid south-west region of Bechuanaland and most of the Great Karoo, and as a result their distribution patterns take on a characteristic trifurcated shape, radiating out from the tropical north-east. Only seven of the forty tropical forms occur in South West Africa, and the distribution of less widespread forms is illustrated by *Chiromantis xerampelina* Peters and *Bufo carens* Smith (Figs. 3 and 4). Such forms show a characteristic bifurcated pattern, one arm extending down the east coast and another up the Limpopo basin towards Griqualand West. It is notable that of the twenty tropical forms that pass south of the Tugela River in Natal, ten also extend inland to the Mafeking area in this way. Forms showing this bifurcated pattern appear to be governed largely by summer conditions, since summer temperatures in the Mafeking area and the east coast are similar, while the Mafeking area

is much colder in winter. The bifurcated pattern is brought about by these forms tending to avoid the highveld, which is cooler both in summer and winter. This pattern cannot be correlated with the rainfall pattern, although clearly the western margin is determined mainly by the aridity of the Kalahari.

Other tropical forms, including the great majority of the treefrog family (Rhacophoridae), are further restricted in that they do not extend far up the Limpopo basin, although they extend some distance down the eastern coastal lowlands of South Africa (e.g. *Hyperolius pusillus* (Cope), Fig. 5). Approximately one-third of the tropical forms are confined to the area experiencing a tropical climate in Köppen's sense (Poynton, 1960). *Xenopus muelleri* Peters provides an example of a tropical distribution pattern (Fig. 6). All the other tropical forms considered above are ones which contribute to the subtraction margin of the tropical fauna, which lies outside the tropical region.

An extraordinary pattern is shown by two tropical species of *Pyxicephalus* Tschudi. Both species are very widespread, but neither occurs in the Natal and Pondoland lowlands. The bullfrog (*P. adspersus* Tschudi) displays this pattern well (Fig. 7). The cause of this anomaly is completely obscure.

The Transitional Patterns. The Natal and Pondoland lowlands carry eight endemic forms, the majority of which are closely related to tropical forms. *Arthroleptis wahlbergi* Smith is a typical example (Fig. 8). Eastern Southern Rhodesia is a similar subtropical centre of endemism (e.g. *A. xenodactyloides* Hewitt, Fig. 8), and this area shares some non-tropical forms with the South African eastern plateau slopes.

Another transitional group is centred in the Natal highlands and the south-eastern Cape lowlands, e.g. *Breviceps adspersus pantheri* Werner, Fig. 9. This subspecies occurs above the 4,000 ft. contour in Natal, the tropical nominate form occurring below this level. The 13° C mean midwinter isotherm runs along this contour in Natal, and it marks a zone where the fauna changes from being predominantly tropical to being predominantly temperate. Fig. 10 gives an interesting example of a tropical form (*Afraxalus b. brachycnemis* (Boulenger)) which has apparently given rise to a tropical transitional form (*A. spinifrons* (Cope)) on the lowlands, and a temperate transitional form (*A. knysnae* (Loveridge)) in the Natal highlands and the south-eastern Cape.

The Natal Drakensberg shows a relatively high incidence of very localized endemics, there being four forms confined to this escarpment. The Amatola Mountains have two endemic forms, and there is one endemic on the Transvaal Drakensberg (Woodbush). Such very localized endemics are unusual amongst the Amphibia. Seven eastern transitional forms cover most of Natal and the eastern Cape, and also a part of the Transvaal, e.g. *Pyxicephalus natalensis* Smith (Fig. 11) and *Rana f. fasciata* auct. (Fig. 12). *R. fasciata* also has a relict population on the Southern Rhodesian highlands.

Of the western transitional forms, one group extends from Angola and Northern Rhodesia to the border area of southern Africa, or beyond into South West Africa and/or Southern Rhodesia (e.g. *Xenopus laevis poweri* Hewitt, Fig. 13). Another group of seven forms occurs on portions of the western plateau slopes (e.g. *Cacosternum namaquense* Werner, Fig. 14).

The Temperate Pattern. Two representatives of the Cape fauna cover all of southern Africa except the Mozambique plain, the central Kalahari and the Namib desert (e.g. *Xenopus l. laevis* (Daudin), Fig. 15. *Rana grayi* Smith is more restricted (Fig. 16) but it has left relict populations in eastern Rhodesia and the arid west. *Kassina wealii* Boulenger leaves the Cape only on the moist eastern highlands (Fig. 17). Six temperate forms in this way pass beyond the area of the proposed Cape region (Poynton, 1960), the area of this region being occupied by, among others, *Hyperolius horstoki* (Tschudi) (Fig. 18). Two-thirds of the Cape forms, however, have restricted ranges within the Cape region, the majority being confined to an area within a hundred-mile radius of Cape Town.

It is notable that typical relict distribution patterns are shown by temperate and transitional forms, but not by any tropical forms. This situation is a clear indication that Southern Africa as a whole has recently been warming up. Amphibian distribution does not necessarily indicate a significant increase in aridity as well, although this is suggested by the distribution pattern of *Rana grayi* in the west.

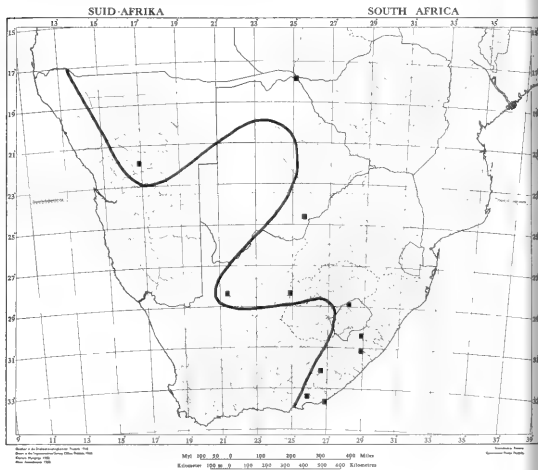


Fig. 1. *Phrynobatrachus natalensis* (Smith). Only marginal localities shown.

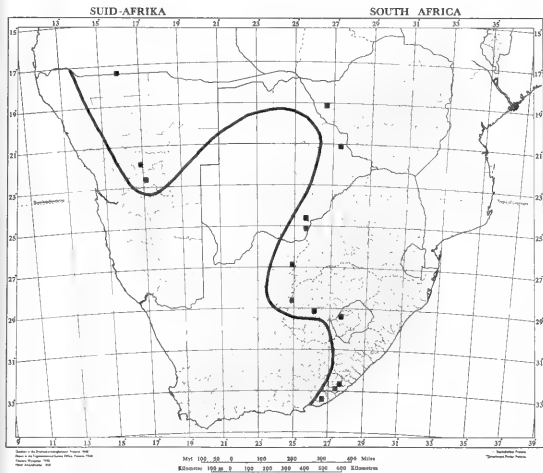
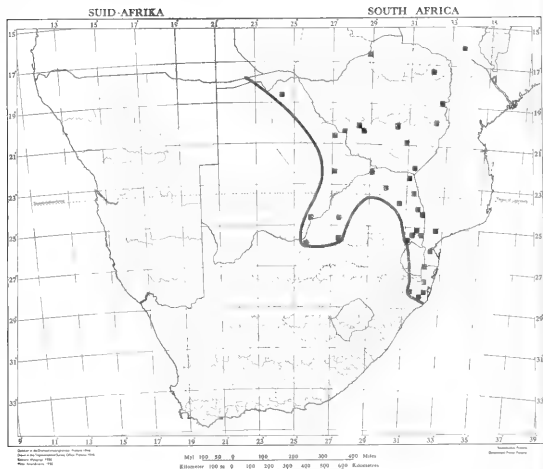


Fig. 2. *Kassina senegalensis* (D. & B.). Only marginal localities shown.

Fig. 3. *Chiromantis xerampelina* Peters.

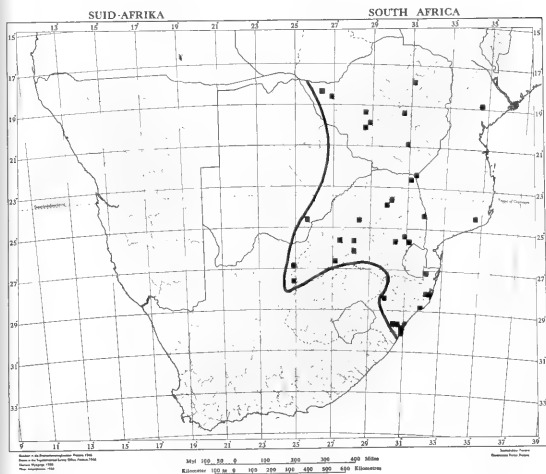
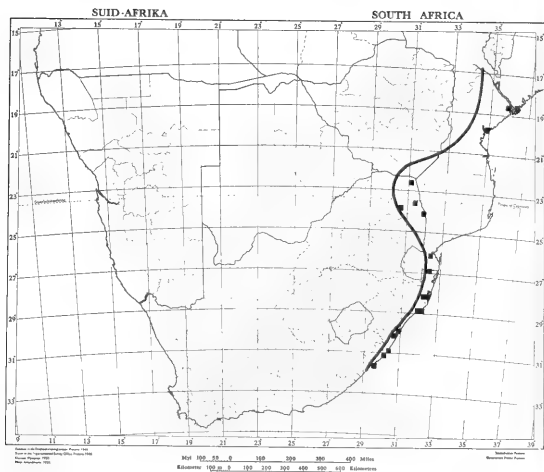
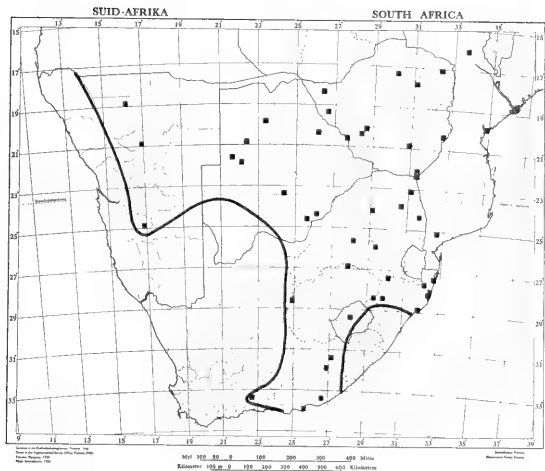


Fig. 4. *Bufo carens* Smith.

Fig. 5. *Hyperolius pusillus* (Cope).

Fig. 7. *Pyxicephalus adspersus* Tschudi.

PATTERNS IN THE DISTRIBUTION OF THE SOUTHERN AFRICAN AMPHIBIA

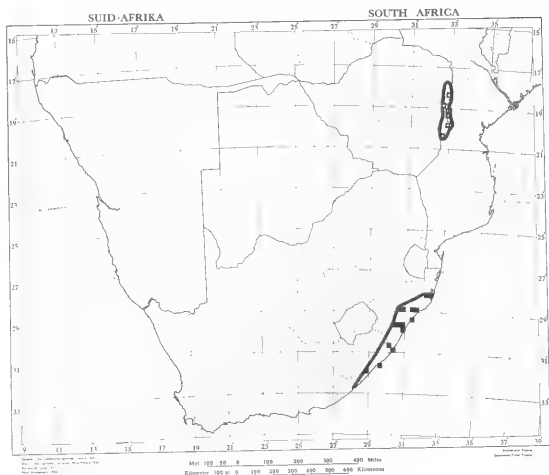
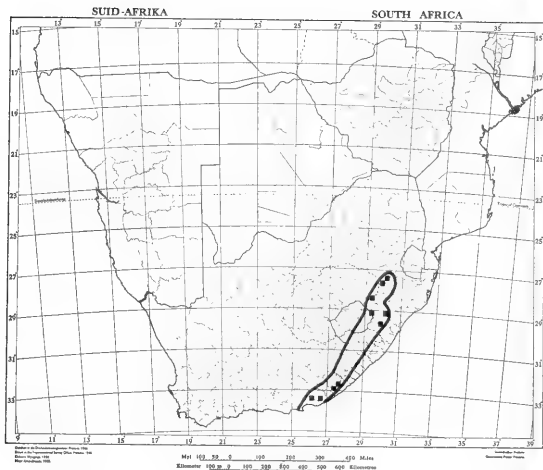
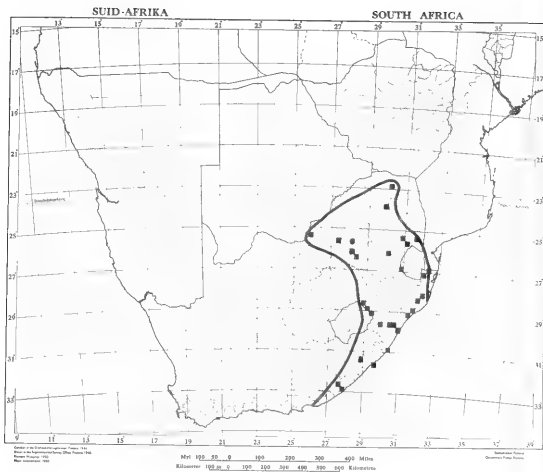


Fig. 8. ■ *Arthroleptis wahlbergi* Smith.
□ *Arthroleptis xenodactyloides* Hewitt.

Fig. 9. *Breviceps pentheri* Werner.

Fig. 11. *Pyxicephalus natalensis* Smith.

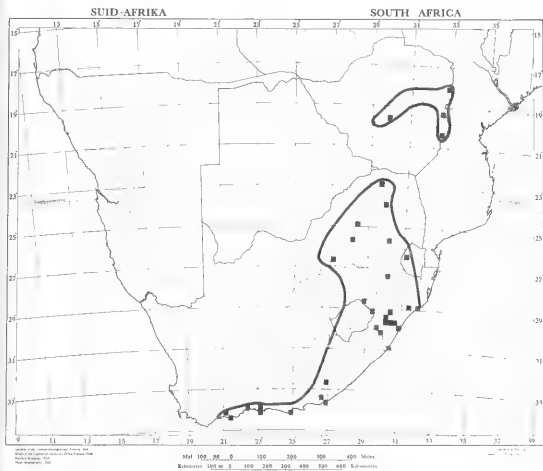
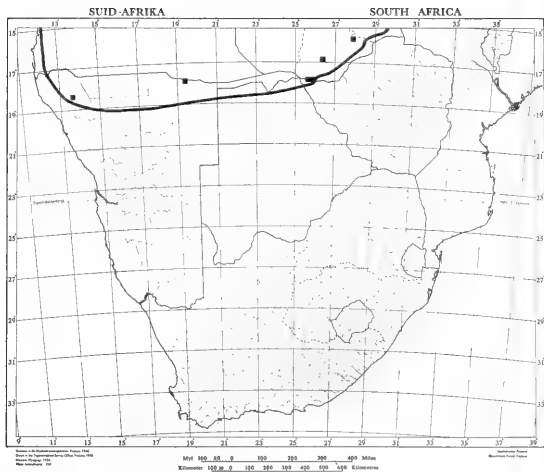


Fig. 12. *Rana fasciata* auct.

Fig. 13. *Xenopus laevis poweri* Hewitt.

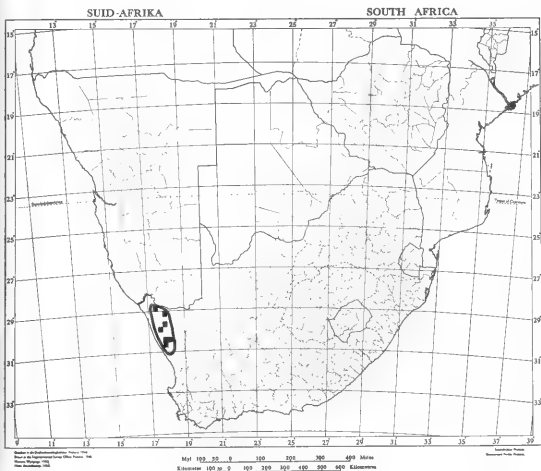


Fig. 14. *Cacosternum namaquense* Werner.

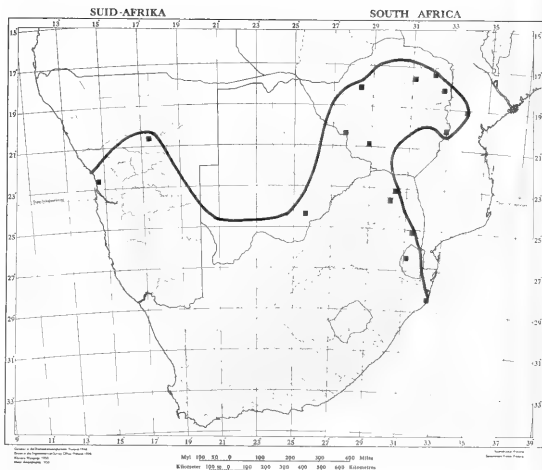


Fig. 15. *Xenopus l. laevis* (Daudin). Only marginal localities shown.

PATTERNS IN THE DISTRIBUTION OF THE SOUTHERN AFRICAN AMPHIBIA

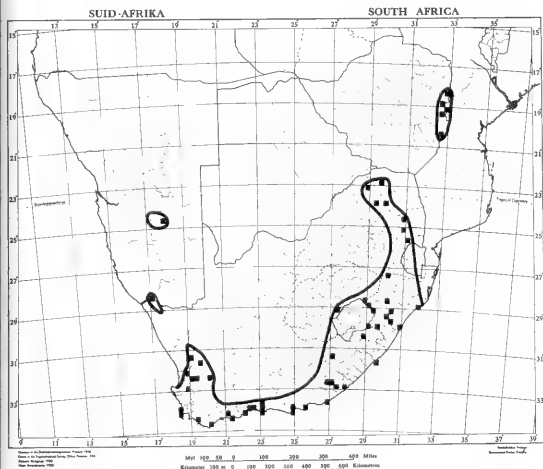
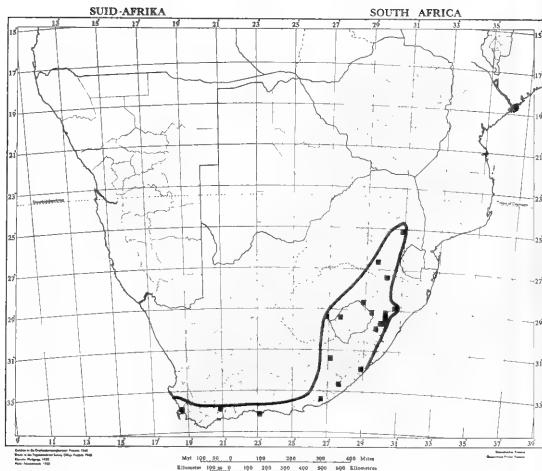


Fig. 16. *Rana grayi* Smith.

Fig. 17. *Kassina wealii* Boulenger.

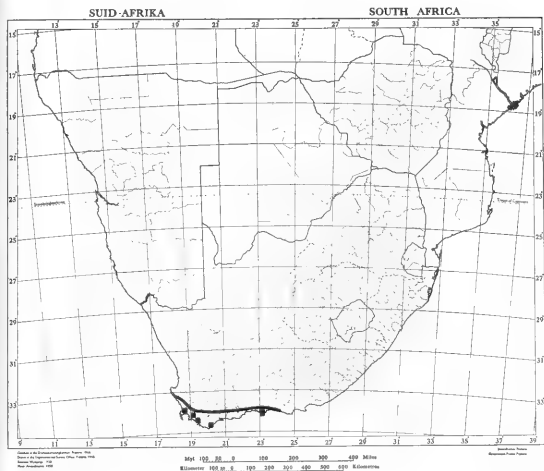


Fig. 18. *Hyperolius horstoki* (Tschudi).

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DISCUSSION

- Prof. Ewer*: I understand that the 4,000 ft. contour in Natal, which coincides with the 13° C mean midwinter isotherm, also marks the line above which wattles can be grown and below which they cannot. (Dr. Poynton confirms and adds that trout also do not come below this line.) The point I wish to make is that these animals are amphibian and thus likely to be affected by the fact that the highlands tend to be particularly wet and misty and also by the fact that the character of the waters, especially running waters, differs above and below 4,000 ft. Many frogs are extraordinarily fussy in regard to the type of water in which they will oviposit. In mentioning these matters, I am seeking an alternative to the postulated correlation with temperature. I think the controlling factor might be something else. I do not believe that animals are as sensitive as thermometers; and I think that putting animal distribution on a map and looking for other matching things, also on maps, tends to be misleading and to obscure other correlations.
- Dr. Poynton*: I agree that to say that distribution matches temperature is not to answer the problems. However, I can find no correlation with moisture at the 4,000 ft. level, nor with any other factor that might affect amphibian distribution. Further, several of our frogs are not strictly tied to water, but even species of such genera as *Breviceps* and *Arthroleptis* tell the same story. Thus, whether or not the eggs are laid in water the same pattern emerges.

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and

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The distribution
of invertebrates
endemic to acid streams
in the Western
and Southern Cape Province

A hydrobiological survey of the Great Berg River in the Western Cape Province (Harrison and Elsworth, 1958) showed that there were characteristic animal communities present in the mountain and upper foot-hill reaches. This is usual for most rivers which have a mountain source and the characteristic species are presumed to have a preference for very clean, siltless water and lower temperatures.

Similar surveys in the Eastern Cape, Natal (Oliff, 1960) and the Transvaal (unpublished results of the National Institute for Water Research) show that similar communities are to be found in upper river reaches in these regions but that a whole group of species found in the Western Province does not recur. These are mainly Ephemeroptera and Trichoptera but other groups are also represented. Sampling of other mountain and upper foothill streams in the Western Cape and records collected by Barnard (1931 to 1947) indicated that these characteristic species appeared to be limited to acid-water streams originating in the Table Mountain Sandstone System, specially in regions of high rainfall; it was therefore expected that they would also be found in the acid streams of the Southern Cape in the neighbourhood of George, Knysna and the Tsitsikamma Forest.

During March, 1960, faunal samples were taken and field pH measurements were made in this southern Cape Region; acid, near neutral and alkaline streams were studied:

1. To determine if the distinctive elements of the fauna of the acid upper streams of the Berg River catchment, and of other acid streams near Cape Town, extended along the Table Mountain Sandstone formations to the limit of their extent near Port Elizabeth.
2. To determine the extent to which this distinctive "Table Mountain Sandstone association" was associated with low pH, i.e. if it was truly "acidobiontic" as suggested by the Berg River studies.
A secondary purpose was:

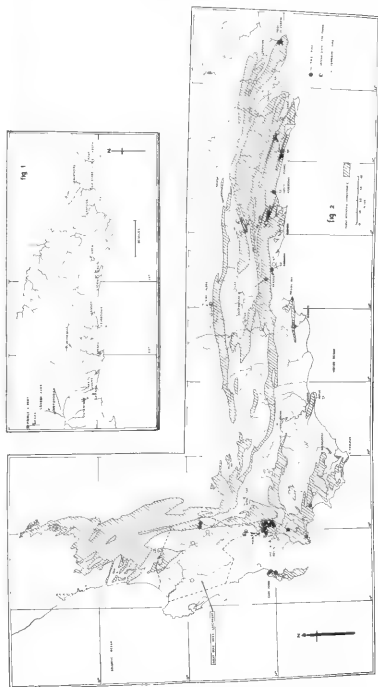
3. To determine the extent to which temperate or "High Veld" species had penetrated the non-acid streams of the region. Only a limited number had been found in the lower, non-acid zones of the Great Berg River.

Sampling stations are shown on Fig. 1. Faunal samples were collected with standard nets (23 mesh cm) and pH readings were taken with a Lovibond Comparator, using standard

* Now at Zoology Department, University College of Rhodesia and Nyasaland.

TABLE I
SAMPLING STATIONS

Station	Remarks	River Type
Kruis River ..	Fast current connecting deep pools. Stony bottoms with growths of <i>Wardia hygrometrica</i> in torrents. Marginal <i>Prionium serratum</i> .	Stongly acid (pH = 5.0 - 5.9), unbuffered water with low total dissolved solids, peat stained.
Kaaimans River	Stony runs, and quieter pools with sand bottoms containing leaves and stones. <i>P. serratum</i> and <i>Scirpus prolifer</i> present	
Outeniqua Pass	Small mountain trickle with <i>Wardia hygrometrica</i> and other moss.	
Storms River ..	Similar to Kruis River above Marginal <i>Scirpus prolifer</i> and <i>Prionium serratum</i> present	
Groot River ..	Just above estuarine influence. Shallow stony run and marginal <i>Scirpus prolifer</i> and <i>S. fluitans</i> .	
Dorps River ..	Mountain stream. Stony runs with moss and roots in interstices. <i>P. serratum</i> present	Slightly acid (pH = 6.0 - 6.9) clear water.
Krom River ..	Stony runs and marginal vegetation, <i>P. serratum</i> <i>S. fluitans</i> etc., Heavy gelatinous growths on both stones and vegetation (Chlamydotrys). Polluted?	
Assegaaibosch	Small shaded tributary of Krom above. Stones in current.	
van Staden ..	Stream at bottom of pass. Small stony runs and deeper quiet pools with marginal vegetation. (<i>P. serratum</i> etc)	
Near Kaaimans	Small shaded stream entering Touws River. Shallow stony runs.	
Keurbooms River	Foothill stream with shallow stony runs and vegetations.	
Buffelsnek near Knysna ..	Mountain stream with shallow stony runs and vegetation in current.	
Between Avontuur and Uniondale	Mountain stream—stones in current and marginal vegetation.	
Upper Swartkops River above Uitenhage (Sept. 1958) ..	Stream in valley about 10 miles above Groendal Dam. Stony runs and pools. Vegetation: <i>P. serratum</i> , <i>Scirpus prolifer</i> , <i>S. fluitans</i> , <i>Nymphaea stellata</i> etc.,	
Grobbelaars ..	Broad open river with stony runs. Little marginal vegetation. <i>Prionium serratum</i> present.	Alkaline (pH = 8.5) clear water.



Figs. 1 and 2.

Fig. 1. The sampling stations, indicated by arrows.

Fig. 2. The distribution of the faunas and the Table Mountain Sandstone, discussed further in the text.

indicators. One water sample from a typically brown acid stream was analysed. The results are preliminary in nature but are compared with those from the Great Berg River, from the Swartkops River, near Uitenhage, and from the upper Buffalo River near King Williams Town.

Sampling Stations (Fig. 1, Table 1)

In Table 1 all the localities visited have been classified into river types with short notes on habitat and vegetation. The streams have been classified according to the pH of the water measured at the time, i.e. strongly acid, pH below 6.0, weakly acid, pH 6 to 7, and alkaline. It was found possible to correlate the pH with the geology to some extent, as discussed later. In presenting the biological results the samples have been grouped according to this scheme.

Chemical Results (Table 2)

It was not the intention of this survey to give a detailed picture of the water quality of the region but merely to relate faunal associations with pH readings. However, Table 2 gives the water analysis from one of the strongly acid streams, the Storms River, as well as analyses from the upper Great Berg River, the weakly acid upper Swartkops River and the upper Buffalo River, Eastern Cape. The results show the unbuffered nature of the water of the acid streams, specially the Storms River, and that the dissolved solids were mainly chlorides. Detailed pH values are shown in Fig. 2. Experience from the upper Berg River shows that the pH in these unbuffered acid streams varies considerably though within a definite range, from this experience the snap pH values have been used to classify the streams in Table 1.

TABLE 2
MINERAL ANALYSIS OF WATER

	Upper* Berg River	Storms River	Upper Swart- kops	Upper Forest Head Streams	Buffalo† Just above Maden Dam
pH	4.3-6.8	—	6.8-7.2	6.5-6.7	7.2
Total Dissolved Solids, p.p.m.	10.0-78.0	68.0	110.0	19.0-26.0	35.0
Total Alkalinity as p.p.m. CaCO ₃	1.0-5.6	0.0	4.6	—	8.8
Total Acidity p.p.m. CaCO ₃	—	13.0	—	—	—
Sulphate, p.p.m. SO ₄	0.0-3.0	4.0	6.5	—	1.1
Chloride p.p.m. Cl	3.0-14.0	25.0	52.0	6.5-7.0	10.0
Total hardness p.p.m. CaCO ₃	1.0-6.7	14.0	24.0	—	11.8
Calcium, p.p.m. Ca	0.1-1.5	2.0	2.4	—	2.4
Magnesium, p.p.m. Mg.	0.0-1.5	3.6	7.2	—	1.4
Sodium, p.p.m. Na	—	14.0	28.0	—	—
Potassium, p.p.m. K.	—	0.4	0.9	—	—

* Harrison and Ellsworth, 1958.

† By permission of the City Engineer (City of East London, February 1961).

THE FAUNA

The fauna of the strongly acid, peat-stained waters

Tables 3, 4, 5 and 6 give the percentage analyses of the faunal samples from the various stations and from the following biotopes respectively:

Stones in fast current,
Moss (*Wardia hygrometrica*) on rocks in torrent,
Stones in quiet backwater,
Marginal vegetation.

TABLE 3
PER CENT ANALYSIS OF FAUNA OF STONES IN CURRENT
(acid peat stained rivers)

		Outeniqua Pass	Kruis River	Kaaimans	Storms	Groot	Remarks
<i>Nemouridae</i> ..	<i>Aphanicercopsis</i> type nymphs ..	38.8	14.2	14.9	15.0	7.4	Not classifiable to spp. Not classifiable to spp.
	<i>Aphanicercella</i> type nymphs ..	—	0.8	2.1	—	3.8	
<i>Baetidae</i> ..	<i>Baetis harrisoni</i> ..	—	—	—	17.7	3.8	
	<i>Pseudocloeon vinosum</i> ..	—	11.8	19.9	1.5	1.3	
<i>Leptophlebiidae</i> ..	<i>Aprionyx peterseni</i> ..	0.9	—	—	—	—	
	<i>Castanophlebia calida</i> ..	4.4	9.3	1.2	1.2	5.1	
<i>Ephemerellidae</i> ..	<i>Lithoglossa penicillata</i> ..	—	6.3	1.5	0.4	5.8	
<i>Megaloptera</i> ..	<i>Chloronella</i> sp. ..	—	0.5	0.5	0.2	0.3	
	<i>Platycheilus</i> sp. ..	—	0.6	—	P	—	
	<i>Taeniochauliodes</i> sp. ..	0.6	—	—	—	—	
<i>Sericostomatidae</i> ..	<i>Barbarochthon</i> cf. <i>brunneum</i> ..	—	2.1	0.6	0.6	—	Species determination difficult.
	<i>Dyschimus</i> sp. ..	0.6	—	—	—	P	
	<i>Petroplax</i> sp. ..	—	—	—	—	—	
	<i>Sinton</i> cf. <i>hageni</i> ..	1.2	—	—	—	—	
<i>Leptoceridae</i> ..	<i>Athripsodes</i> sp. near <i>bergensis</i> ..	—	1.7	0.3	—	19.6	
	<i>Leptoceridae</i> ..	4.7	—	—	—	—	
<i>Hydropsychidae</i> ..	<i>Sciadurus</i> cf. <i>obtusum</i> ..	4.4	—	—	—	—	
	<i>Cheumatopsyche afra</i> ..	—	—	—	0.8	—	
	<i>Cheumatopsyche thomasseti</i> ..	—	—	—	1.4	—	
<i>Polycentropodidae</i> ..	<i>Polypsectopus</i> sp. ..	0.3	0.2	—	—	—	
	(Berg River type)	—	—	—	—	—	
<i>Philopotamidae</i> ..	<i>Chimarra</i> spp. ..	—	1.2	8.8	14.3	2.6	
<i>Rhyacophilidae</i> ..	<i>Agapetus agilis</i> ..	—	—	1.4	1.8	0.3	
<i>Elmidae</i> ..	<i>Berg River Type GBG 8J</i> ..	1.8	12.5	0.4	7.4	2.9	
	<i>Berg River Type GBG 6AA</i> ..	21.2	13.2	2.2	7.5	13.4	Mostly <i>Stenelmis</i> <i>Limnius</i> and larvae.
<i>Ptilodactylidae</i>	—	1.8	—	P	—	
<i>Helidodae</i> ..	sp. A ..	—	—	17.5	P	0.1	
	sp. B ..	—	1.1	P	P	—	
<i>Simuliidae</i> ..	<i>Simulium</i> larvae ..	—	—	5.6	9.9	2.6	
<i>Total Chironomidae</i>	9.8	7.5	10.4	3.5	27.9	
<i>Rhagionidae</i> ..	<i>Atherix</i> -type larvae ..	—	1.5	1.2	—	1.6	
<i>Anura</i> ..	<i>Heleophryne</i> sp. ..	P	P	—	P	—	
	Total ..	88.7	87.5	92.5	82.6	98.5	

Note: Species in italics — acid water, endemic forms.

In all cases species were identified as far as possible and those species common to the upper Great Berg River and these streams, but absent elsewhere, have been underlined. The underlined species are considered to be endemic to acid waters of the Western and Southern Cape.

As will be seen these underlined endemic species usually form an appreciable part of the fauna in all habitats sampled from the strongly acid streams.

The Fauna of slightly acid streams

These were all clean, unpolluted and non-turbid streams in the same region, but mainly further from the coast. Three were mountain streams, i.e. Dorps, near Prince Albert, Assegaibos stream and the Buffelsnek stream, and the latter two were only a few miles from strongly acid streams with the typical fauna. Results are given in Tables 7 and 8 from the following biotopes:

Stones in fast current,
Marginal vegetation.

TABLE 4
PER CENT ANALYSIS, MARGINAL VEGETATION FAUNA
(acid, peat stained rivers)

		Kruis	Kaaimans	Storms	Groot
		%	%	%	%
<i>Nemouridae</i>	<i>Aphanicercopsis</i> (type)	—	5.4	—	—
	<i>Aphanicercella</i> (type)	3.2	0.9	0.8	P
<i>Baetidae</i>	<i>Austroclaeon africanum</i>	—	—	—	59.4
	<i>Pseudoclaeon vinosum</i>	40.2	—	2.3	—
<i>Caenidae</i>	<i>Caenidae</i>	—	0.9	—	P
<i>Ephemerellidae</i>	<i>Lithogloea harrisoni</i>	4.4	P	1.5	—
	<i>Lithogloea penicillata</i>	3.7	—	—	—
<i>Odonata</i>	Total Anisoptera	0.2	7.2	3.1	—
	Total Zygoptera	0.7	6.3	—	—
<i>Leptoceridae</i>	<i>Athripsodes</i> spp. near <i>bergensis</i>	19.7	39.9	41.7	1.4
	<i>Athripsodes</i> spp.	—	1.8	—	—
<i>Sericostomatidae</i>	<i>Barbarochthon brunneum</i>	0.7	6.3	6.8	—
<i>Elmidae</i>	8J	0.7	—	1.5	1.4
	6AA	0.9	—	3.0	1.4
	Others	0.2	—	—	—
<i>Ptilodactylidae</i>	Larvae	0.1	1.8	1.5	—
<i>Helodidae</i>	sp. A	—	0.9	—	—
	sp. B	3.0	—	—	—
<i>Chironomidae</i>	Total	17.6	9.9	33.4	33.8
		92.3%	81.3%	95.6%	97.4%

Note: species in *italics*—acid water endemic forms.

Again the acid water endemic species have been underlined and it will be noted that in the stones in the current (Table 7) there are far fewer in the weakly acid streams well within the endemic region, and that there are none at all in similar streams on the fringe of the endemic region. In the marginal vegetation no acid water endemic species were found at all. (Table 8). The fauna of these streams is more typical of neutral to alkaline streams in temperate parts of the country. However, it is a depleted fauna and appears to consist of those species which can stand the slightly acid pH. Many of them are actually an important part of the fauna of the strongly acid streams as well and those which are not have been marked on the tables.

The fauna of alkaline streams

Only one truly alkaline stream was sampled, the Grobbelaar's River between Oudts-
hoorn and the Congo Caves, which had a pH of 8.5. It is a foothill stream. The faunal
associations are given in Tables 9 and 10. Both the fauna of the stones in the current and
of the marginal vegetation were found to be typical of alkaline streams of the High Veld
of the Transvaal and the upland regions of Natal.

TABLE 5
STRONGLY ACID STREAMS. MOSS (WARDIA HYGROMETRICA) IN TORRENT
(Per cent analysis)

					Upper Berg River (Zone 1*)	Kruis River
					%	%
<i>Nemouridae</i>	<i>Aphanicercopsis</i> -type nymphs	2.0	17.5
<i>Baetidae</i>	<i>Acentrella capensis</i>	1.0	—
	<i>Pseudocloeon vinosum</i>	—	17.6
<i>Leptophlebiidae</i>	<i>Castanophlebia calida</i>	1.0	0.01
<i>Ephemerellidae</i>	<i>Lithogloea</i> sp. <i>Berg River</i> sp. <i>B.</i>	26.3	1.2
<i>Megaloptera</i>	<i>Chlorionella</i> sp.	—	0.01
	<i>Platychauliodes</i> sp.	1.0	0.04
<i>Trichoptera</i>	<i>Barbarochthon brunneum</i>	0.5	0.3
	<i>Petrothrincus triangularis</i>	3.5	—
	<i>Athripsodes</i> — <i>A. bergensis</i> type	—	0.01
	<i>Sciadorus</i>	1.5	—
<i>Hydraenidae</i>	Total	5.0	0.01
<i>Elmidae</i>	<i>Berg River</i> type 8J	6.5	16.2
	<i>Berg River</i> type 6AA	4.5	—
	<i>Berg River</i> type 128A	3.5	—
	Others	0.5	2.6
<i>Simuliidae</i>	<i>Simulium medusaeforme</i>	10.1	0.5
<i>Total Chironomidae</i>		29.3	40.0
					96.2	95.9

*Taken in November, 1950, with a coarser net—11 mesh/cm.

Note: italic species—acid water endemic forms.

DISCUSSION

Two distinctive faunal associations were found in clean, permanent streams in the area surveyed:

1. Table Mountain Sandstone, acid water association; details of this are given in appendix 1. This occurred in streams with a pH below 6 and was similar to that which has been studied in detail in the upper parts of the Great Berg River. Many of the characteristic species of this association appear to be limited to acid water only but others may merely be species demanding rigidly oligotrophic (very clean) conditions. The association also includes a number of fairly ubiquitous non-pH-sensitive species such as *Baetis harrisoni*, *Afronurus harrisoni* and *Pseudocloeon vinosum*. No aquatic snails occur but *Pisidium* spp. are found.

TABLE 6
STRONGLY ACID STREAMS. BACKWATERS

		Kruis River	Kaaimans River
		%	%
<i>Copepoda</i>	<i>Cyclops</i> spp.	4.1	—
<i>Hydrachnellae</i>	Various species	1.4	3.5
<i>Nemouridae</i>	<i>Aphanicerella</i> type nymphs	0.7	5.9
	<i>Aphaniceropsis</i> type nymphs	1.5	15.2
<i>Baetidae</i>	<i>Austroclaeon</i> sp.	—	2.4
	<i>Pseudocloeon</i> sp. (<i>Berg River</i> sp. A)	49.5	—
	<i>Pseudocloeon vinosum</i>	6.6	—
<i>Leptophlebiidae</i>	<i>Aprionyx peterseni</i>	2.6	—
	<i>Choroterpes nigrescens</i>	—	1.2
	<i>Castanophlebia calida</i>	—	1.2
<i>Ephemerellidae</i>	<i>Lithogloea penicillata</i>	2.2	—
<i>Ecdyonuridae</i>	<i>Afronurus harrisoni</i>	1.9	—
<i>Zygoptera</i>	<i>Allocnemis leucosticta</i>	—	17.6
<i>Trichoptera</i>	<i>Barbarochthon brunneum</i>	0.3	4.7
	<i>Athripsodes</i> sp. cf. <i>bergensis</i>	12.1	18.8
	<i>Chimarra</i> sp.	—	2.4
	<i>Polypectropus</i> sp.	2.9	—
<i>Elmidae</i>	<i>Berg River</i> type 6AA	5.8	10.6
<i>Ptilodactylidae</i>	0.3	1.2
<i>Helodidae</i>	<i>Berg River</i> sp. A	—	1.2
<i>Chironomidae</i> (total)	6.2	9.4
		97.9	95.3

Note: italic species—acid water endemic forms.

DISTRIBUTION OF INVERTEBRATES ENDEMIC TO ACID STREAMS OF WESTERN AND SOUTHERN C.P.

2. Temperate climate association. This term is used for want of a better one, as this association has been found in all permanent streams in High Veld and other temperate parts of the country. It is best developed in definitely alkaline streams, such as the Grobbelaars River.

Some of the species comprising it are also found in weakly acid streams along with the non-pH-sensitive species mentioned above. Details of this association are given in appendix 2.

Both these association types show considerable "internal variations" in that the species composing them vary according to the river zone where they are found. For instance special species appear in the upper mountain streams in the Table Mountain System as shown by the fauna of the stream on the Outeniqua Pass, Table 4.

TABLE 7

PER CENT ANALYSIS—STONES IN CURRENT FAUNA. CLEAR, SLIGHTLY ACID RIVERS

		Dorps	Krom	Assegani-Bosch	Buffelsnek	Near Touw R.	After Avontuur*	Keurbooms*	V. Stadens	Upper Swartkops
		%	%	%	%	%	%	%	%	%
<i>Perlidae</i>	† <i>Neoperla spio</i>	—	—	—	0.3	—	—	—	—	—
<i>Nemouridae</i>	<i>Aphaniceroopsis</i> (type)	9.5	3.3	—	—	16.3	—	—	—	—
	<i>Aphaniceroella</i> (type)	2.0	—	2.0	—	—	—	—	—	—
<i>Baetidae</i>	<i>Acentrella cf. capensis</i>	0.2	—	—	—	0.2	—	—	—	—
	<i>Baetis harrisoni</i>	0.8	0.7	8.1	2.1	—	P	P	—	9.7
	<i>Baetis bellus</i>	—	—	—	—	—	P	P	—	—
	<i>Centroptilum sudafricanum</i>	14.1	—	25.2	10.1	8.2	P	P	4.7	—
	† <i>Centroptilum varium</i>	0.1	—	—	—	—	—	—	—	—
	† <i>Centroptiloides bifasciata</i>	—	2.3	—	—	—	—	—	—	—
	<i>Pseudocloeon maculatum</i>	—	15.4	—	—	—	P	—	—	0.6
	<i>Pseudocloeon vinosum</i>	—	4.6	—	1.5	—	—	—	0.1	—
<i>Leptophlebiidae</i>	<i>Adenophlebia peringueyella</i>	0.7	—	6.6	1.6	4.0	P	P	0.1	—
	<i>Castanophlebia calida</i>	2.5	—	—	—	0.4	—	—	—	—
<i>Ephemerellidae</i>	<i>Lithogloea penicillata</i>	—	—	5.6	0.3	—	—	—	—	—
<i>Tricorythidae</i>	† <i>Neurocaenis discolor</i>	9.5	—	—	2.1	—	—	—	—	—
<i>Ecdyonuridae</i>	<i>Afronurus harrisoni</i>	—	—	—	3.7	—	—	—	—	—
<i>Leptoceridae</i>	<i>Athripsodes</i> spp.	0.7	—	P	—	P	—	—	—	—
<i>Hydropsychidae</i>	<i>Cheumatopsyche afra</i>	3.5	11.8	2.0	4.2	2.7	P	P	0.8	3.8
	† <i>Cheumatopsyche thomasseti</i>	—	—	—	2.4	—	—	—	—	—
	<i>Macronema</i> sp.	—	10.2	0.5	—	—	—	—	0.1	—
<i>Philopotamidae</i>	<i>Chimarra</i> sp.	8.5	—	—	1.3	5.5	—	—	—	—
<i>Hydroptilidae</i>	<i>Hydroptila</i> sp.	P	—	—	—	—	P	—	—	—
<i>Elmidae</i>	<i>Elm</i>	2.5	4.0	11.6(?)	—	—	—	—	—	—
	6.4.4	1.3	0.3	—	15.3	9.3	—	P	—	—
	(Others)	3.9	3.0	—	—	—	—	—	—	—
<i>Helodidae</i>	<i>Helodid</i> sp. A	0.8	2.6	—	—	4.6	—	—	—	—
	<i>Helodid</i> sp. B	0.8	0.3	—	—	—	—	—	—	—
<i>Simuliidae</i>	<i>Simulium</i> larvae	7.6	3.0	P	11.3	26.2	P	P	73.1	73.7
<i>Chironomidae</i>	Total Chironomidae	8.9	34.4	21.6	19.5	14.4	P	P	9.4	5.8
<i>Rhagionidae</i>	<i>Atherix</i> type larvae	1.0	—	2.0	—	—	—	—	—	—
		78.8	95.9	85.2	72.0	91.8	—	—	88.3	93.6

*N.B.—At these two stations, per cent analyses are not available. P indicates presence, (not necessarily in small numbers in these two columns)

†Species not found in strongly acid streams.

Note: italic species acid water endemic forms.

Extent of the Table Mountain Sandstone, acid water ("acidobiontic") association

Sampling stations visited during this survey have been plotted on Fig. 2, together with a few stations studied previously on the Swartkops River, near Port Elizabeth and all the Stations used during the survey of the Great Berg River. In addition a few other scattered records have been plotted. The pH readings have been inserted next to the station when available except in the case of the Great Berg River. It will be noted that the faunal type is indicated symbolically according to the key.

What is here called the Table Mountain Sandstone, acid water fauna was found to extend to very near the eastern limit of the T.M.S., especially in the acid, peat-stained, dystrophic waters of the George-Tsitsikamma region. The fauna is obviously one of very acid streams and these are only found flowing off T.M.S. formations.

As has been already pointed out, this fauna appears to be not only associated with the acid conditions but with conditions of high rainfall. If it were to appear anywhere else in the country it would be expected in the mountain regions of the Eastern Cape Province and specially in the Amatola Mountains where the rainfall is high and south temperate forest, similar to the Tsitsikamma Forest, occurs. Samples were taken in the upper Buffalo River and its headwater streams in the Amatola Mountains in January, 1961 (Table 11). Although the pH of the water of the headwater streams was slightly acid and that of the upper Buffalo neutral, (Table 2) none of the acid water species, endemic to the Western and Southern Cape, recurred.

TABLE 8
PER CENT ANALYSIS—MARGINAL VEGETATION FAUNA
CLEAR, SLIGHTLY ACID RIVERS

		Krom	Buffels- nek	Near Avon- tuur*	Keur- booms*	V. Stadens
		%	%	%	%	%
<i>Nematoda</i> ..	Nematodes	—	31.1	P	P	8.5
<i>Nemertea</i> ..	†Prostoma sp.	6.3	6.4	P	P	5.3
<i>Baetidae</i> ..	<i>Baetis bellus</i>	10.6	—	P	—	—
	<i>Centroptilum excisum</i>	—	0.3	P	—	—
	<i>Centroptilum sudafricanum</i>	4.3	0.4	P	P	—
	<i>Pseudocloeon vinosum</i>	8.5	3.6	—	—	—
<i>Coenagrionidae</i>	<i>Pseudagrion</i> sp.	6.3	3.4	P	P	—
<i>Hydroptilidae</i>	<i>Oxyethira</i> (= <i>Argyrothorax</i>) <i>velocipes</i>	6.3	3.4	—	P	11.2
	<i>Hydroptila</i>	P	—	—	P	—
<i>Simuliidae</i> ..	<i>Simulium</i> larvae	10.6	13.8	P	P	1.8
<i>Chironomidae</i>	Total	14.9	26.4	P	P	34.0
<i>Mollusca</i> ..	† <i>Burnupia</i> sp.	2.1	2.3	P	P	—
		69.9	91.1	—	—	60.8

*% figures not available.

P indicates presence, not necessarily in small numbers, in these two columns.

†Not found in strongly acid streams.

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TABLES 9 AND 10

THE FAUNA OF GROBBELAARS RIVER (ALKALINE RIVER)
PER CENT ANALYSIS

TABLE 9 STONES IN CURRENT	%	TABLE 10 MARGINAL VEGETATION	%
Planaria	1.8	Prostoma	1.3
Nematoda	1.6	Nematoda	3.9
Lumbricidae	0.2	Lumbricidae	4.1
Potamon cf. sidneyi	0.4	Hydrachnellae	1.3
Hydrachnellae	10.9	Caenidae	1.9
Baetis harrisoni	28.3	Austroclaeon sp.	4.9
Pseudocloeon maculosum	7.7	Baetis bellus	1.1
Caenidae	1.6	Centroptilum excisum	1.1
Adenophlebia peigueyella	0.8	<i>Centroptilum indusii</i>	0.2
Euthraulus elegans	7.1	Centroptilum pulchrum	0.2
Afronurus harrisoni	4.4	Baetid juveniles	32.1
Aeschna sp.	0.2	Euthraulus elegans	0.1
Ecnomus sp.	0.2	Micronecta piccanin	1.3
Cheumatopsyche afra	0.6	Micronecta juvs.	43.7
Cheumatopsyche thomasseti	9.1	Strina sp.	0.1
Orthotrichia sp.	3.8	<i>Psephenidae (Eubrianax)</i>	0.1
<i>Psephenidae (Eubrianax)</i>	2.2	Corynoneura spp.	1.9
Simulium larvae	1.8	Pisidium sp.	0.7
Orthocladiinae	8.9		100.0
Other Chironomidae	6.5		
Tabanidae	1.6		
Burnupia	0.2		
	99.9		

Note: species in italics are found in northern and eastern South Africa but this is the first record for the S.W. Cape region.

Weakly acid streams in the Southern Cape had a mixed fauna, mainly of non-pH-sensitive forms (see Appendix 3) with a few acid water forms, when connected to an acid stream, and a few of the more resistant species normally found in alkaline streams in temperate parts of the country (appendix 2). Very often, as was the case in the Van Staden's Pass stream and the upper Swartkops River, the fauna could be looked on as a somewhat depleted "temperate" association.

Penetration of "Temperate" species

As previously mentioned the fauna of the alkaline parts of the Great Berg River, and of other alkaline streams in the Western Cape Province, is composed of species which are found in the streams of the temperate High Veld of the Transvaal and O.F.S. and the uplands of Natal. (See Oliff, 1960). However, many species found in the latter areas are not found in the Great Berg, not even in the lower reaches where the pH is neutral to alkaline. This survey has shown that a number of these "missing species" are present in the eastern part of the Cape System Region. These include *Centropilum varium*, *Centropilum indusii*, *Centropiloides bifasciata*, *Neoperla spio*, *Eubrianax* sp., and *Simulium bequaerti*. Some of these are also found in the warmer region of South Africa.

It must be pointed out that it is difficult to delineate the various associations clearly at present as the taxonomy of a number of groups still has to be worked out; these include the Hydrachnellae, Trichoptera, Chironomidae and Dryopoidea. Progress is being made with all these except the last.

TABLE 11
FAUNA OF UPPER BUFFALO RIVER, KING WILLIAMS TOWN
STONES IN CURRENT

	Forest head stream Evelyn Valley 26/1/1961	Buffalo just above Maden Dam 23/1/1961
	%	%
Nematoda	0.5	0.9
Tubificidae	3.8	—
Hydrachnellae	1.0	0.9
Aphanicercopsis-type nymphs	15.0	0.9
Baetis harrisoni	—	0.1
Acentrella natalensis	7.9	—
Centropilum sudafricanum	7.1	2.6
Neurocaenis sp.	2.3	10.4
Castanophlebia calida	9.7	—
Euthraulus elegans	—	0.1
Cheumatopsyche afra	5.1	3.1
Cheumatopsyche thomasseti	—	0.9
Oxyethira veloxipes	1.8	—
Hydroptila capensis	—	0.1
Eubrianax sp.	—	0.2
Helodidae	6.1	—
Simulium larvae	11.2	41.5*
Pentaneura spp.	0.5	0.4
Other Chironomidae mostly Orthoclaadiinae	11.7	23.7
Corynoneurinae	3.0	5.1
Bezzia-type larvae and pupae	1.6	—
Rhagionidae	—	1.4
Empididae	3.1	—

*A pupa of *Simulium impukane* de M. was present.

(The authors thank Miss P. Hoal of The East London Municipality, who assisted with these samples).

SUMMARY

1. The results of faunal sampling of streams in the Southern Cape are presented, together with some considerations of river chemistry in this region.
2. On the basis of these results and other data (some published), it is shown that there is a fauna endemic to the acid streams of the Southern Cape.

APPENDIX 1

Preliminary list of Table Mountain sandstone, acid-water species (South Western Cape). This list is built mainly from the survey of the Great Berg River and other records from the Western Cape Province. Species marked "E" were found during the recent survey of the eastern part of the Cape System Region, those marked (e) by previous workers in this eastern area, (mainly Barnard 1931, 1932, 1934A, 1934B, 1937, 1940 and 1947).

PLECOPTERA

Nemouridae (Leuctridae)

Aphanicerca capensis Till. (e)
Aphanicerca uncinata Barnard
Aphanicerca lyrata Barnard
Aphanicerca bicornis Barnard
Aphanicerca bovina Barnard
Aphanicerca tereta Barnard
Aphanicerella barnardi Till
Aphanicerella scutata Barnard
Aphanicerella bifurcata Barnard
Aphanicerella nigra Barnard
Aphanicerella quadrata Barnard

Aphaniceropsis denticulata (Till).
Aphaniceropsis tabularis Barnard
Aphaniceropsis outeniquae Barnard (e)
Aphaniceropsis hawaquae Barnard

Desmonemoura pulchellum Till. (e)

EPHEMEROPTERA

Baetidae

Pseudocloeon sp. A (E) (Berg River)

Leptoptelebiidae

Aprionyx peterseni (Lest.) (E)
Aprionyx tabularis (Eaton)
Aprionyx pellucidulus (E.-P).
Castanophlebia albicauda Barnard

Aprionyx intermedius Barnard (e)
Aprionyx rubicundus Barnard (E?)

Ephemerellidae

Ephemerellina barnardi Lest.
Lithogloea harrisoni Barnard (E)
Lithogloea sp. A (Berg River) (E)

Lithogloea penicillata Barnard (E)
Lithogloea sp. B. (Berg River)

(Note: the specimens of *L. Harrisoni* reported from the Amatola Mountains by Crass, 1947, appear to belong to another species which extends from this locality, in montane regions, through Natal and the Transvaal to Nyasaland and possibly further).

ODONATA

Brinck, 1955b, lists *Presba piscator* Barnard (Anisoptera) and *Ecchlorolestes peringueyi* (Ris), *E. nylephtha* Barnard, *Chlorolestes conspicua* Sélys and *C. umbrata* Sélys (Zygoptera) as being endemic to the South-Western Cape Region. It is not known, however, if any of these are limited to acid streams, they are all mountain species.

MEGALOPTERA

Corydalidae

Chloroniella peringueyi E.-P. (E) (e)
Platychniodes tenuis (MacLach.) (e)
Platychniodes woodi Barnard (e) (E?)

Platychniodes capensis Barnard
Platychniodes thorni Barnard

TRICHOPTERA

Dyschimus thymmerifer Barnard
Sinion hageni Barnard (E?)
Rhoizema saxiferum Barnard
Rhoizema spinosum Barnard
Aselas camella Barnard
Petroplax caricis Barnard
Petroplax prionii Barnard
Barbarochthon brunneum Barnard (e) (E)
Hydrosalpinx sericea Barnard
Petrothrincus circularis Barnard
Athripsodes schoenobates (Barnard) (e) (E)
Athripsodes promontorii (Barnard)
Athripsodes cedri (Barnard)
Athripsodes sylvaticus (Barnard)
Athripsodes securis (Barnard) (e)
Athripsodes amplexus (Barnard)
Athripsodes oryx (Barnard)
Athripsodes elaphus (Barnard)
Athripsodes bibulus (Barnard)
Athripsodes dieseli (Barnard)
Athripsodes bergensis Scott (E)
Leptechno scirpi (Barnard)
Leptechno helicotheca Scott
Oecetis modesta (Barnard) (e)
Homilia elephas Barnard
Sciadorus acutus Barnard
Polypsectropus sp. (E?) (Berg River species)
Chimarra ambulans Barnard (e) (E)
Chimarra georgensis Barnard (e)
Thylakion urceolus (Barnard) (e)
Agapetus agilis (Barnard) (E)

Dyschimus collyrifer Barnard (e)

Rhoizema montanum Barnard (e)
Rhoizema furciferum Barnard
Cheimacheramus caudalis Barnard
Petroplax phleophila Barnard (e)
Petroplax curvica Scott

Petrothrincus triangularis Barnard
Athripsodes tabularis Barnard
Athripsodes longistylis (Barnard)
Athripsodes potes (Barnard) (e)
Athripsodes scramasax (Barnard)
Athripsodes tuckeri (Barnard)
Athripsodes corrivalis (Barnard)
Athripsodes stephanus (Barnard) (e)
Athripsodes caricarcia (Barnard)
Athripsodes spatula (Barnard)
Athripsodes prionii Scott

Leptechno lupi (Barnard)

Oecetis lucipetens Barnard
Homilia knysnaensis (Barnard) (e)
Sciadorus obtusus (Barnard) (e) (E?)

Chimarra cerceris Barnard

Thylakion forcipatum Barnard
Agapetus murinus (Barnard).

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COLEOPTERA

Gyrinidae

Brinck, 1955a, in his monograph on Southern African Gyrinidae lists 15 species of Gyrinidae, mostly Aulonogyrus, endemic to the Cape System Region. It is not known if these are affected by the pH of the water though most of them are confined to T.M.S. mountains.

Hydraenidae

There appear to be many species found only in acid streams of this region but none of them has been described. J. Balfour-Browne is producing a monograph.

Dryopidae

Strina sp GBG. 7U (E)

GBG species 128A
(Berg River species)

Elmidae

GBG. 8J (E)
GBG. 125E (E)
GBG. 3M

GBG. 6AA (E)
GBG. 230C
GBG. 81B
(Berg River species)

Helodidae

Berg River sp. A (E)
Berg River sp. C (E?)

Berg River sp. B (E)

DIPTERA

Blepharoceridae

Elporia barnardi (Edw.) (e)
Elporia spinulosa Edw.
Elporia capra Barnard

Elporia capensis Edw.
Elporia uniradius Barnard (e)

Simuliidae

Probably no species are limited to acid stream except, perhaps, *Simulium hessei* Fr. & de M. which has only been found in T.M.S. mountains.

Chironomidae

Of the 80 or so species recorded by Scott (1958) from the Great Berg River and other localities in the Western Province, none is known to be limited to acid streams, and most are found in other parts of South Africa.

HYDRACHENELLAE

It is possible that some of the species described by Viets from acid waters in the Western Province are "acidobionts" and limited to T.M.S. streams and pools. The following are suggested.

Plesiohygrobatas pectinipalpis Viets
Atractides pulcher Viets
Ambiguobates permixtus Viets
Ambiguobates (Ambiguobatella) peltophorus Viets
Tortipalpus obscuriporus Viets.

Atractides coriaceus Viets
Diversibates pilosus Viets

The specimens collected on the last expeditions still have to be worked up.

A number of the species listed in this appendix may not be truly acid water species but oligotrophic (clean water species) and endemic to the Cape System mountains. Many, probably, can be considered to belong to a palaeogenic, montane element, e.g. the Nemouridae, the Ephemerellidae, the Odonata, the Corydalidae, some Trichoptera and the Blepharoceridae; other cannot, e.g. the Baetidae, Leptophlebiidae and certain caddis, Athripsodes spp. and Chimarra spp.

APPENDIX II

"Temperate" species which appear to prefer alkaline water. Some are also found in slightly acid streams. This is a preliminary list of those found in the Cape System Region. New records for the region, found during the recent survey of the eastern part are marked (N).

NEMERTINI

Prostoma sp.

MOLLUSCA

<i>Lymnaea natalensis</i> (Swartkops R.) Kraus	<i>Bulinus tropicus</i> Kraus
<i>Lymnaea columella</i> Say. (exotic from U.S.A.)	<i>Anisus natalensis</i> (Kraus)
<i>Burnupia stenochoria</i> M + P	<i>Burnupia gordonensis</i> M + P
<i>Ferrissia connollyi</i> Walker	
<i>Tomichia ventricosa</i> Rve.	
<i>Pisidium costulosum</i> Conn.	

INSECTA PLECOPTERA

Perlidae

Neoperla spio (Newm.) (N)

EPHEMEROPTERA

Baetidae

<i>Baetis bellus</i> Barnard (also sub-tropical)	<i>Baetis</i> sp. A Berg River
<i>Baetis</i> sp. B. Berg River	<i>Centroptilum sudafricanum</i> Lest.
<i>Centroptilum varium</i> Crass (N)	<i>Centroptilum indusii</i> Crass (N)
<i>Centroptilum pulchrum</i> Crass	<i>Centroptiloides bifasciata</i> E.-P. (N)
<i>Cloeon lacunosum</i> Barnard	

Caenidae

Too little is known of this group to place the species.

Tricorythidae

Neurocaenis discolor Burm.

Leptophlebiidae

Euthraulus elegans Barnard.

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TRICHOPTERA

Cheumatopsyche thomasseti (Ulmer)	
Macronema sp. (? natalensis Ulmer)	Ecnomus spp.
Dipseudopsis capensis Wlkr.	

COLEOPTERA

Psephenidae

Eubrianax sp. (N)

Numerous Dytiscidae, Hydrophilidae, Hydraenidae, Dryopidae and Helmididae almost certainly belong here but not enough is known of their distribution and taxonomy at the moment to place them.

DIPTERA

Simuliidae

Simulium ruficorne Macquart	Simulium bovis de Meillon
Simulium bequaerti Gibbins (N)	Simulium alcocki Pomeroy (Swartkops River).
Simulium hirsutum Pomeroy (Swartkops River)	

Chironomidae

Scott (1958) gives a full list of the species found in the acid and alkaline parts of the Great Berg River.

APPENDIX III

Species which appear not to be pH-sensitive. Most are limited to the temperate parts of the country, others are also found in sub-tropical parts (U). This is a preliminary list of those found in the Cape System Region.

DECAPODA

Potamon perlatus-sidneyi complex (U)

EPHEMEROPTERA

Baetis harrisoni Barnard	Centroptilum excisum Barnard (U)
Pseudocloeon vinosum Barnard	Austrocloeon virgiliae Barnard (U)
Austrocloeon africanum Barnard (U)	Acentrella capensis Barnard
Adenophlebia peringueyella Lest and other species	
Castanophlebia calida Barnard	Choroterpes nigrescens Barnard
Afronurus harrisoni Barnard	

TRICHOPTERA

Athripsodes harrisoni Barnard	
Cheumatopsyche afra (Mosely)	Oxyethira (syn. Argyrobothrus) velocipes (Barnard) (U)
Hydroptila capensis (U)	
Orthotrichia sp (U)	

DIPTERA

Simuliidae

Simulium medusaeforme Pomeroy
Simulium impukane de Meillon (U)
Simulium unicornutum Pomeroy (U)
Simulium nigratarsis Coquillett (U)

Simulium harrisoni Fr. & de M.
Simulium merops de Meillon
Simulium adersi Pomeroy (U)

Note: The following groups have not been considered in these appendices: all Crustacea below Decapoda, all Heteroptera, all Dytiscidae, Hydrophilidae and Hydraenidae. Chironomidae are only known from the Western Cape Province and from the Swartkops River, near Port Elizabeth and not from the rest of the region. The distribution of Odonata is discussed by Brinck, 1955b.

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DISCUSSION

- Mr. Grindley:* Macan (Biol. Rev. 36: 151) concludes that pH is of no significance as a factor limiting the distribution of freshwater animals, except in the case of certain protozoa. What does Dr. Harrison think about this? Do the mountain streams of the South-west Cape form a very special case?
- Dr. Harrison:* Yes, perhaps a case rather special to South Africa. In the Transvaal an artificial situation has been created by the breakdown of pyrites in the gold mines. As a result one may find streams with a pH of about 2.9 for about 20 miles. Much life is eliminated but they are carpeted with sphagnum moss and *Baetis harrisoni* and chironomids occur. This indicates that pH does play a part. Again, in Zeekoewel where the pH goes to 10, certain animals are restricted. Dr. Cholnoky can name the

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pH of a given water just by examining its diatoms, judging not by individual species but on the percentage composition of the flora. We have checked him a number of times and have always found him right.

Prof. Ewer: I understand that, although *Baetis harrisoni* may occur in acid streams, it is not restricted to them. Are there any organisms which are so restricted?

Dr. Harrison: Not that I know of. There is a chironomid in the Transvaal which occurs in neutral or slightly acid waters and seems happiest in acid streams, but none are completely restricted.

Prof. Ewer: This work of Harrison's is potentially of great ecological importance because pH has, as Mr. Grindley says, fallen into disrepute as a possible limiting factor. I would like to see it now taken a stage further and experimentally treated to determine whether the important factor is really acidity or something else often associated with it, such as organic content of the water.

Dr. Harrison: While organic matter might be important, some of the acid streams are peaty but others are not.

Dr. Stuckenberg: This paper brings out very clearly that, as far as stream-breeding species go, we are often dealing with two different animals: the larval and adult stages. This work is chiefly concerned with the eco-geography of larvae.

TAXONOMIC ADDENDUM

Since going to press, the following new names have become available:

For <i>Pseudocloeon</i> sp. A	read <i>Pseudocloeon saxophilum</i> Agnew.
For <i>Beatis</i> sp. A	read <i>Beatis glaucus</i> Agnew.
For <i>Beatis</i> sp. B	read <i>Beatis latus</i> Agnew.

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J. (OMER - COOPER

GRAHAMSTOWN.

The distribution of the
Cape Province *Dytiscidae*
and speculations as to their
possible origins ✕

The Dytiscidae are a family of carnivorous aquatic Coleoptera found in rivers, streams and ponds. Some prefer running water, others still, but none are rigidly restricted to one or the other. That they go back a long way in time may be inferred from the fact that many of their genera are world wide in distribution. That they have existed in Africa for a long period seems probable since, with the exception of the genera endemic to the Cape Province, all but four genera, and at least forty species, are known to occur also in Madagascar.

It is true that the Dytiscidae can fly but there is no evidence that they can cross deserts or any wide stretch of sea. The indications, in fact, are all to the contrary. Apart from one *Cybister* taken from a puddle on the east coast of England in 1829 there are no records of even casual invasions of Dytiscidae from the continent. *Hyphydrus ovatus* Linn. common in the south of France has not been able to reach either Corsica or the opposite Mediterranean coast. *Hyphydrus aethiopicus* B-B., common and widely distributed in Africa south of the Sahara, has not appeared in Madagascar and there are many other examples which could be cited. The Dytiscidae do not normally ascend to great heights in their flight and it seems probable, since they often dive on to glass roofs, that they find water by sight. If, then, they found themselves over the sea it seems likely that they would descend and their long survival be improbable. The correspondence between the Dytiscid fauna of Africa and Madagascar seems too great to be accounted for by chance, and leads to the conclusion that either a connection between that island and the continent persisted for a longer time than is now considered possible, or that some of the species have persisted for a longer period of time than seems reasonable.

As little beyond the general outlines of the biology of the African Dytiscidae is known, the problem has been approached from the geographical point of view. An attempt has been made to ascertain the distribution of the species within the Cape Province and, by comparison with their distribution in Africa and beyond, to make tentative suggestions as to their origin. Since there have been so few specialist collectors and the taxonomy of the group is difficult, the picture must be incomplete and not necessarily accurate.

The Dytiscid fauna of the Cape Province, as at present known to me, consists of 117 species divided into 31 genera. Of these genera 12 are world wide, 4 are only found in the Old World, 3 are now predominantly Holarctic, 4 are known only from Africa and Madagascar and 8 are endemic to South Africa. Of the 117 species, 63 are endemic to southern Africa, (which is taken here to include South West Africa, Bechuanaland, Southern Rhodesia,

Southern Mozambique, Swaziland and Basutoland) and of these 63, 44 are known only from the Cape Province.

For purposes of analysis the fauna was divided into:—

- I. A basic Cape fauna comprising those species which are common everywhere.
- II. Species also widely distributed but occurring less frequently in collections.
- III. Species only recorded from the Eastern Cape.
- IV. Species recorded only from the Western Cape.

The division between the two sides of the Cape Province was taken arbitrarily as a line running from the Storms River mouth north to the Orange River. Species occurring frequently on the western side with only a few records a short way to the east of the boundary are considered as Western Province endemics and *vice versa*.

I. The basic Cape fauna

This comprises 14 species belonging to 10 genera. Only one genus (*Tyndalhydrus*) is endemic to South Africa and it is monospecific. The remaining genera are widespread in Africa and outside it. Of the 14 species, none of which occur also in Madagascar, 9 have a limited distribution outside South Africa and, as far as my experience goes, the density of their populations falls quickly and progressively to the northern parts of their range. These species perhaps originated in South Africa. The remaining five species have a wide distribution in Africa and are probably tropical in origin.

II. Rarer species

To this group 25 species belonging to 16 genera have been attributed. Of the genera, one (*Sharphydrus*) is endemic to the Cape Province, two (*Africophilus* and *Canthyporus*) occur only in Africa and Madagascar, three (*Potamonectes*, *Agabus* and *Rantus*) are now predominantly Holarctic, seven are world wide in the tropical and temperate zones and three occur in the Old World only.

Of the 25 species, 11 are endemic to Southern Africa. One, *Africophilus jansei* O-C. is reported from Swaziland, Basutoland, the north of the Eastern Province and Uniondale in the Western Province; Two, *Rantus peringueyi* Rég. and *Potamonectes vagrans* O-C., are endemic to South Africa; Seven, *Potamonectes capensis* O-C., *Sharphydrus coriaceus* Rég., *Canthyporus hottentotus* Gem. and Har., *Canthyporus petulans* Guign., *Canthyporus testaceus* Zimm., *Rantus cicurus* Fab. (all with a western bias in the Cape) and *Yola inopinata* O-C., are endemic to the Cape Province. The remaining species are tropical, most of them aethiops, but *Hydaticus exclamatoris* Boh. and *Eretes sticticus* Linn., the latter world wide in the tropics and sub-tropics, reach West Africa north of the equator and Madagascar.

III. Species recorded from the Eastern Province only

In this group are 51 species belonging to 19 genera of which only one, *Tikoloshanes* may be endemic to South Africa. (Since the only species of this genus stands in some collections under *Eretes*, its distribution may be wider than is at present known). Of the 51 species no less than 12 appear to be endemic to the Eastern Cape and 10 more are recorded only from southern Africa. With the exception of the *Canthyporus* spp. (to be discussed later) all the endemics belong to wide-spread genera, have a more or less restricted and continuous distribution and have probably arisen *in situ* from their relatives. Apart from *Africophilus nesiotis*, Guign., the remaining species are invaders from the tropics; 15 of them reach West Africa north of the equator and seven are also present in Madagascar. The majority of these species, whether they occur in West Africa, Madagascar or not, appear only on the coastal strip or, if they have spread inland, are not found south of the approximate latitude of East London.

It would seem that some barrier is operating to hinder their spread, perhaps temperature or the scarcity of permanent water.

The genus *Africophilus* is a specialized member of the tribe *Laccophilini* whose main genus, *Laccophilus*, is world wide in distribution. The species of *Africophilus* have a specialized habitat, that of mud and gravel beside mountain streams or in trickles over rock faces where algae afford cover and foothold. They have, further, a discontinuous distribution; one is known from the Ivory Coast, one is endemic to the Cape Province, one is endemic to Madagascar and *A. nesiotis* is known both from the mountains of the north-eastern Cape and Madagascar. This suggests that it has inhabited the region for a longer time than need be postulated for the other species, tropical or autochthones.

IV. Species confined to the Western Province

The western Cape fauna is exceedingly interesting. Of its 27 species, 25 are endemic. (*Canthyporus exilis* Boh. was originally recorded from Caffraria and *Coelhydrus brevicollis* Shp. from Port Elizabeth but neither have since been taken from their type localities). The 25 species belong to 12 genera of which six are endemic to the Western Cape. Five of these are monospecific and belong to the tribe *Hyphydrini* whilst the sixth, *Sharphydrus* has two species, one confined to the Berg River system, and one whose range extends into the eastern side of the Western Province. The fauna is dominated by species of the genus *Canthyporus* and 14 of these are endemic. The remaining endemics belong to genera with a wide distribution in Africa and outside it.

The particular problems presented here are numerous. *Bidessus mundulus* O.-C., (in press), *Herophydrus obscurus* Shp., and *Copelatus platynotus* Rég. may well have been derived from other species of their genera present in the fauna. This may also be true of *Laccophilus immundus* Shp. and *Herophydrus capensis* Shp. but both are very distinct species, neither belonging to any of the species complexes present in their genera. Why do both appear to be confined to a very small area around Cape Town? The genus *Canthyporus* has a very discontinuous distribution, one species in South West Africa, one in the Belgian Congo, one in Tanganyika, one in Madagascar, one in Swaziland, one in Basutoland, and 21 in the Cape Province of which three are endemic to the eastern Cape and 14 to the western Cape. This distribution possibly indicates an ancient genus which may have arisen in south central Africa at a time when the climate was more temperate; was driven out by increasing desiccation and rising temperature, leaving species in the north now confined to the mountains, and has undergone intensive speciation in the Cape where the present temperature range and abundant permanent waters provide ideal conditions for it.

The five species of the *Hyphydrini* genera, *Andex insignis*, *Hydropeplus trimaculatus*, *Darwinhydrus solidus*, *Coelhydrus brevicollis*, *Primospes suturalis*, with the exception of *Andex insignis* which has not to my knowledge been taken since it was first recorded, are very common in the South Western Cape and a few specimens of each have been taken as far west as Witte-elsbosch in the Humansdorp district. They are different in appearance from each other and from the main genus, *Hyphydrus*, which has many species in the Old World. They are usually regarded as relicts from a very ancient fauna, a view supported by the fact that there are related genera in South America where *Hyphydrus* does not occur, which have, however, undergone speciation, and one in tropical Africa with three species, one in West Africa and the Belgian Congo, one in the Southern Sudan and one in Madagascar. *Andex insignis* shares with *Tyndalhydrus caraboides* an unusual feature which may be primitive, that of the failure of the prosternal process to meet the metasternal process. It is difficult to understand why all of these genera are each only represented by one species.

Finally there remains the question of the Holarctic genera present. These are represented by *Agabus raffrayi*, *Rantus capensis* and two endemic *Rantus* spp. together with *Potamonectes*

capensis and *Potamonectes vagrans*. The Holarctic elements in the Cape fauna are usually regarded as recent immigrants from the north. Of *Agabus raffrayi* this is no doubt true. There are *Agabus* spp. in Abyssinia and records of this species from Abyssinia to the Cape. This genus is not represented in Madagascar. The genus *Rantus* has, however, several species in Madagascar and is also present in South America and Australia. *R. capensis* also has records from Abyssinia to the Cape. The two endemic species are closely related to it. There are more species of *Rantus* in Central Africa than of *Agabus* and fewer in Abyssinia. Is it not more probable that *Rantus*, rather than being of Holarctic origin, has been in Africa as long as the majority of the genera and, if we accept a Gondwanaland origin for those with a world wide distribution, should we not bracket it with them?

The origin and present distribution of the two species of *Potamonectes* is extremely puzzling. The genus is now predominantly Holarctic. A few species reach Central America, there are several in the Southern Sudan, Abyssinia and Eritrea but none in Africa between those and these in the Cape. There are none in Madagascar nor in Australia. That they are related to the European and North American *Potamonectes* seems certain since *P. capensis* possesses two preapical denticles on the elytra as do members of one group of the northern species. *P. capensis* is common in the Western Cape but extends a little to the east of its boundary; *P. vagrans* occurs in the south of the Transvaal, the Orange Free State, and the Eastern Cape, its range overlapping in the centre with that of *P. capensis*. Both *Potamonectes* spp., *Sharphydrus coriaceus* and *Tyndalhydrus caraboides* live in rivers and dams, often the same ones where their ranges overlap. If they are ancient inhabitants why should *P. capensis* and *S. coriaceus* be almost restricted to the western Cape, *P. vagrans* to the eastern whilst *T. caraboides* has conquered the whole Province? That the spread of a species may be slow is likely, since, besides the hazards of rivers in spate and dams drying up, the larval mortality, especially in the younger stages, must, because of the carnivorous habit of both larvae and adults amongst which they live, be great. One would have supposed however that the time available to them has been ample for at least a coincidence of their ranges.

Species attributed to each group. Southern African endemics are marked ***, South African endemics **, and Cape Province endemics *.

I. *Laccophilus cyclopis* Shp., *Laccophilus lineatus* Aubé, *Hyphydrus aethiopicus* B-B., *Herophydrus oscillator* Shp., *Guignotus infirmus* Boh., *Guignotus lineolatus* Boh., *Clypeodytes meridionalis* Rég., ***Yola subopaca* Rég., ***Tyndalhydrus caraboides* Shp., *Copelatus erichsoni* Guer. var. *marginalis* Gschw., ****Copelatus capensis* Shp., *Hydaticus galla* Guer., *Hydaticus servillianus* Aubé., *Rantus capensis* Aubé.

II. *Hydrocoptus aethiopicus* B-B., *Laccophilus pellucidus* Shp., *Laccophilus congener* O-C., *Laccophilus concisus* Guign., ****Africophilus jansei* O-C., *Hydrovatus macrocerus* Rég., **Sharphydrus coriaceus* Rég., **Yola inopinata* O-C., **Bidessus* n.sp., *Bidessus sharpi* Rég., *Guignotus bivirgatus* Guign., **Potamonectes capensis* O-C., ***Potamonectes vagrans* O-C., *Herophydrus iniquatus* Boh., **Canthyporus petulans* Guign., **Canthyporus hottentotus* Germ. and Har., **Canthyporus testaceus* Zimm., *Agabus raffrayi* Shp., **Rantus cicurus* Fab., ***Rantus peringueyi* Rég., *Hydaticus exclamatoris* Aubé, *Hydaticus capicola* Aubé, *Hydaticus caffer* Boh., *Eretes sticticus* Linn., *Cybilster tripunctatus* Ol. subsp. *africanus* Cast.

III. *Hydrocanthus micans* Shp., *Hydrocanthus constrictus* Rég., *Canthydrus sedilloti* Rég., *Canthydrus notula* Er., *Laccophilus contiro* Guign., *Laccophilus adpersus* Boh., **Laccophilus* n.sp., *Philaccolus lineatoguttatus* Rég., *Africophilus nesiotus* Guign., *Hyphydrus cycloides* Rég., **Hyphydrus komghaensis* O-C., *Methles cribratellus* Fairm., **Potamonectes* n.sp.,

Uvarus vitticollis Boh., *Uvarus baoulicus* Guign., *Uvarus peringueyi* Rég., *Guignotus geminodes* Rég., *Guignotus transvaalensis* Rég., *Bidessus ovoideus* Rég., *Bidessus fraudator* O.-C., *Clypeodytes evanescens* Boh., ****Clypeodytes hieroglyphicus* Rég., **Clypeodytes ignobilis* O.-C., *Yola elegantula* Boh., ****Yola simulantis* O.-C., ***Yola swierstrai* Gschw., *Yola frontalis* Rég. subsp. *capensis* O.-C., *Yola tuberculata* Rég., ****Hydrovatus nefandus* O.-C., *Hydrovatus glomeratus* Guign., ****Hydrovatus amplicornis* Rég., ****Hydrovatus validicornis* Rég., **Hydrovatus brownei* O.-C., ****Hydrovatus gravicornis* O.-C., *Hydrovatus pescheli* O.-C., ****Canthyporus swaziensis* O.-C., **Canthyporus cooperae* Guign., **Canthyporus fluvialis* O.-C., **Canthyporus guignoti* O.-C., *Copelatus edax* Guign., *Copelatus sylvaticus* Guign., *Copelatus pulchellus* Klug., **Copelatus* n.sp., **Copelatus* n.sp., **Copelatus* n.sp., *Hydaticus bivittatus* Cast., *Hydaticus dregei* Aubé, *Hydaticus flavolineatus* Boh., *Hydaticus dorsiger* Aubé, *Tikoloshanes eretiformis* O.-C., *Aethionectes apicalis* Boh.

IV. *Laccophilus immundus* Shp., *Herophydrus capensis* Rég., *Herophydrus obscurus* Shp., **Bidessus* n.sp., *Bidessus imitator* O.-C., **Sharphydrus capensis* O.-C., *Hydrovatus galpini* O.-C., **Canthyporus lateralis* Boh., **Canthyporus luridipennis* Rég., **Canthyporus exilis* Boh., **Canthyporus parvus* O.-C., **Canthyporus laccophiloides* O.-C., **Canthyporus bicinctus* Rég., **Canthyporus navigator* Guign., **Canthyporus canthydroides* O.-C., together with six undescribed species of *Canthyporus*; **Andex insignis* Shp., **Hydropeplus trimaculatus* Cast., **Darwinhydrus solidus* Shp., **Coelhydrus brevicollis* Shp., **Primospes suturalis* Shp., **Copelatus platynotus* Rég.

SUMMARY

The picture yielded by this analysis appears to be one of the Cape Province inhabited by a small group of species which probably originated there in comparatively recent times. This supplemented by species from the tropics, some of which, since they occur also in Madagascar, are probably older in origin than others, together with endemics which have arisen from them. Mixed with these are a few species, occurring chiefly in the western Cape which may be representatives of a still older fauna. These are: **Andex insignis* Shp., *Hydropeplus trimaculatus* Cast, *Coelhydrus brevicollis* Shp., *Darwinhydrus solidus* Shp., *Primospes suturalis* Shp., and possibly *Tundalhydrus caraboides* Shp., *Sharphydrus coriaceus* Rég., *Sharphydrus capensis* O.-C., *Potamonectes capensis* O.-C. and *Potamonectes vagrans* O.-C., the two latter being representatives of a now predominantly Holarctic genus.

The presence of practically all of the genera and so many of the species in both Africa and Madagascar indicates (unless we accept, against the evidence of present day happenings, a considerable immigration and emigration between them) an astonishing fixity of species for very long periods of time or a Madagascar more easily available to colonisation at a much later time than is now usually accepted.

DISCUSSION

- Dr. Stuckenberg*: It has been suggested that Madagascar was last connected with Africa during the mid-Jurassic. If this is so, its Dytiscid fauna must surely have flown to the island.
- Dr. Omer-Cooper*: The beetles could possibly be older. One authority has suggested that they go back to the Permian.
- Dr. Stuckenberg*: An interesting feature is the occurrence of *Africophilus nesiotus* on Madagascar and the Drakensberg. More usually the affinities of the Madagascan fauna are with the central African mountains.

S. H. (SKAIFE

HOUT BAY,
CAPE TOWN.

The distribution
of the Argentine Ant
Iridomyrmex Humilis Mayr

The Argentine ant was first collected in 1866 in the neighbourhood of Buenos Aires and was described and named *Iridomyrmex humilis* two years later by the Austrian myrmecologist, Gustav Mayr. Since that date this insect has been spread all round the world by man's commerce and it is now a major pest in many countries on both sides of the equator, but not in the tropics. It was first recorded from South Africa in 1908 by the late C. P. Lounsbury and at that date it was apparently limited to a small area of the Cape Peninsula. One of the first tasks given me when I was appointed entomologist at the Rosebank Experiment Station forty years ago was to carry out some experiments with corrosive sublimate as a means of controlling the pest, whose presence was beginning at that time to make itself felt as an irritating nuisance as far afield as Rondebosch, but I failed to find it in Wynberg or beyond.

Today it is the only ant to be found in the built-up areas of the Cape Peninsula. It has killed or driven off all our native species in areas where it has established itself, with the exception of occasional colonies of the driver ant, *Dorylus helvolus* Linn, which are able to withstand the fierce competition of the Argentinian invader seemingly because of their nomadic habits. There are, however, a few small pockets of land that are still free of the Argentine ant. For example, although the pest is common at Hout Bay, it is not to be found at Llandudno, only two or three miles away, and I am unable to suggest any reason for this. There is also an area amid the vineyards of Constantia where this ant has failed to establish itself, and it is not to be found on the mountain slopes above an altitude of 800 feet or so.

It is now well established in Stellenbosch, Paarl, Wellington, Worcester, Robertson, Clanwilliam, Port Elizabeth, Graaff Reinet, East London and probably many other towns and villages in the coastal region of the Cape Province, but I failed to find it in Durban or Pietermaritzburg during a recent visit. A few small colonies have been found from time to time in Johannesburg and Pretoria, but this species does not seem to flourish at any great altitude above sea level, or in areas where the winter temperature drops below freezing for any length of time. Although it has been recorded from several places in Great Britain during the past fifty years it has not succeeded in gaining a foothold there.

It is nowadays a harmful pest in the southern states of the United States, Madeira, Portugal, Spain, the Riviera and Australia, but there are no reports of it from tropical regions. In its homeland, Brazil and the Argentine, it does not appear to be very troublesome. Entomologists have visited South America to hunt for diseases, parasites and predators that might serve to keep the pest in check, but they have failed to find any—the Argentine ant seems

to be extraordinarily free of natural enemies. During the forty years that I have had this species under observation I have not come across any disease or parasite among them. I have fed colonies with massive doses of the spores of *Nosema apis*, a protozoon that causes heavy mortality among honeybees at the Cape in the spring, but the Argentine ant is quite immune to this parasite; caterpillar wilt diseases and *Isaria* fungus are also innocuous to them. The rapid spread of this insect round the world is doubtless due at least in part to their hardiness and freedom from natural checks, but it is difficult to understand why they have failed to invade the tropics, why they are common at East London but absent from Durban.

In 1918 the late Dr. C. W. Mally put up a memorandum to the authorities urging that a campaign be started immediately to wipe out the pest in the Cape Peninsula. He warned that such a campaign would be expensive, and nothing was done. Today the ant is so widely spread and firmly established that it would be impossible to exterminate it. So far no survey has been made to determine the spread of this species in South Africa. Is it still extending its range and, if so, what are the factors that encourage or limit its distribution? People living in areas not yet invaded might well ask that steps be taken to prevent the further spread of this, the most pernicious ant pest in the world.

DISCUSSION

Dr. Poynton: Ants which appear to be Argentine Ants occur in Pietermaritzburg.

Dr. Stuckenberg: Yes, I can confirm this; and would also add that the Argentine Ant has spread to Mauritius, which is undoubtedly tropical. They have now exterminated all other species of ant occurring in the lowland areas of the island.

Dr. Poynton later sent me specimens of the ants found in Pietermaritzburg that he thought were Argentine ants, but they proved to be another species. S.H.S.

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Patterns of
animal distribution
on the African Continent
(summing-up talk)

We are having this symposium at a time when most profound changes are going on around us, changes which affect society, but which also affect the nature, the fauna and flora in particular. The natural conditions of life are destroyed, and a new order or disorder prevails in their place. Indigenous animals and plants are disappearing from the countries in which they used to be found. Take our cities, or for that matter, the cities in any civilized country. Whatever animal and plant life is left in the cities is of foreign origin: the trees are all exotic, the flowers in the gardens are predominantly so, the animals are by and large gone altogether except for a very few. But even if we turn to the platteland, the picture is not essentially different. Cultivated crops are introduced: mealies, wheat, sugar cane . . . The trees are exotic: European willows, Australian acacias. Even the weeds are foreign: khakibos, cosmos, jointed cactus, prevail. In the forestries we see stands of eucalyptus and pine. In ranching areas more of the natural vegetation is left, but the larger animals are gone to a very great extent. The pattern of animal and plant distribution built up in hundreds of millions of years, is being destroyed almost in the living memory of one generation of men. The peculiar distinctions of different countries are disappearing, and a homogenized and impoverished fauna and flora are taking their place. As Elton (1958) puts it, we are attending at a breakdown of Wallace's Realms—the great zoogeographic areas which used to be so distinct from one another.

Under the circumstances it is the first duty of zoogeographers, or perhaps of biologists in general, to make a concise recording of the present state of the distribution of animals and plants, a recording of conditions which will not be discernible much longer. Once they go, getting information about the past conditions of life on this planet will be practically impossible. For this reason I should like to commend with the greatest satisfaction the work that has been performed by our mammalogists, who have made a detailed survey of the distribution of large mammals in the four provinces of the Republic of South Africa and in South-West Africa. (See papers by Bigalke and Bateman, p. 85, Vincent, p. 110. Kettlitz, p. 118, van Ee, p. 53, van der Spuy, p. 41). The work on small mammals, as reported in further two papers (Davis, p. 56, Meester, p. 77) is catching up with that done on larger animals. The work on the distribution of birds seems to have been carried out in great detail, so that the three speakers on bird distribution have not so much reported new observations, but have sought to correlate the already known distribution with certain factors of climate, vegetation, barriers presented by river valleys, etc. The present distribution of lower verte-

brates seems to be known quite accurately, as can be judged from papers dealing with amphibians (Poynton, p. 252) and fishes (Crass, p. 229, Farquharson, p. 233, Jackson, p. 223). Needless to say, the surveys of animal distribution should be repeated periodically, so that we can be aware of any further changes that are taking place. The state of affairs in respect of invertebrates is not quite as satisfactory. In respect of some groups the information available is fairly complete, but other groups still have not been worked on systematically. Fortunately the lower animals are less affected by the activities of man, and there is still time to make exact records in most cases.

This most urgent task having been performed, inevitably we turn from the registering of facts to the underlying causes. We ask ourselves the great question: why? Why are the animals and plants distributed over the world as they are, or perhaps, as they used to be before the activities of man have thrown everything into a turmoil?

To understand how the animals and plants have become distributed as they are, we cannot do better but to try and study the processes of dispersal of animal and plant species at the present time. In a general way all would agree, that the area occupied by any species is the result of the balance or equilibrium between the tendency of each species to broaden their area of distribution and certain factors which could be referred to as the "environmental resistance". Let us examine these two aspects of animal distribution. I will first deal with the tendency to dispersal.

Random movements of animals must inevitably bring some individuals of a species beyond the area in which the species is established. How far, and how fast can such individuals go? Obviously the movements of dispersal are only indirectly related to powers of locomotion. We know that some birds can cover enormous distances in a matter of a few weeks during their seasonal migrations, but nevertheless keep to restricted areas, and the migrations themselves are limited to fairly narrowly specified routes. On the other hand it is known, that some animals systematically migrate beyond their established areas, even if they cannot survive in the territories they reach, so that their journey is one of no return. It is reported (Ford 1953) that some butterflies such as the Red Admiral *Vanessa atalanta*, and the Painted Lady *Vanessa cardui*, are regularly found in England, although they cannot survive the British winter. Every year in spring they fly across the channel from the Continent.

Specialists in various groups will certainly recall other cases of this kind. I personally have observed something similar with dragonflies in South Africa. In the years from 1950 to 1959 I have kept under very close observation an area on the outskirts of Johannesburg, mainly because I used the pools and small dams scattered in the area as a source of frogs' eggs and embryos for my embryological work, but also in connection with my study of the dragonfly fauna. I came to know the area very well. I was therefore very thrilled one day in March, 1954, to find on one of the pools several specimens, ♂♂ and ♀♀, of a minute dragonfly of the genus *Agriocnemis*. The next year I specially searched the area for further specimens of *Agriocnemis*. None were to be found on the same pool, but in February 1955, I caught 1 on another pool some 500 yards from the first. I have never seen this dragonfly again near Johannesburg, in spite of careful searching. The nearest place I know where the species occurs in abundance is on the Magalaguin River near Potgietersrust. What apparently happened, was that some specimens (or possibly even only one of *Agriocnemis*, which is a very poor flier) were carried by the wind to Johannesburg. A colony was founded here, which persisted at least two years, but did not get established and disappeared.

An analogous case occurred in October 1957, when I observed in the same area a specimen of another dragonfly *Rhyothemis semihyalina*. This is a very conspicuous dragonfly, with black proximal parts of the wings. In flight it is easily recognizable and cannot possibly be overlooked. In the course of a few days I observed several of these dragonflies flying along the pools in my area. They were never seen either before or after. The nearest place where

the species occurs regularly is also the Magalaquin River near Potgietersrust. In this case the dragonflies must have reached Johannesburg, which is far outside the normal range of the species, by active flight, but they failed to establish a colony, as I would certainly have been able to notice their presence in subsequent years had any developed in my pools.

The conclusions that I wish to draw from observations of this kind is that animals will always be found wandering beyond their established range of distribution, and as a rule these wanderings will lead to no permanent effect; the migrants failing to settle permanently, and dying off either immediately, or after a few generations.

We know, however, that under certain circumstances species do increase their area of distribution, and populate areas where the species had not been found previously. It is of importance in connection with the present discussion to know the approximate rates of dispersion of such species. Observations are available in respect of exotic species introduced by man into overseas countries. I would like, however, to quote two examples of the spreading of the area of distribution of species in their own native country. Several British butterflies have shown fluctuations in their area of distribution. Around the beginning of this century they were found only in the south-western counties of England, but later made a recovery and spread out to the north and east (Ford, *loc. cit.*). The Comma *Polygonium C-album* extended its distribution to the east between 1915 and 1953 by about 110 miles, that is about three miles per annum. Almost at the same time, between 1920 and 1953, the White Admiral *Limnitis camilla* extended its distribution to the north by almost 60 miles, that is about one-and-a-half miles per annum. These observations are valuable because they more directly illustrate what may be the rate of distribution of species under perfectly natural conditions.

As I have said, there are many records of the dispersal of species brought into new countries from overseas. The Gipsy Moth *Limntria dispar* was introduced from Europe to North America and in 25 years it spread 220 miles to N.N.W. from Boston where it was brought originally, an average of about nine miles per annum. (Quoted from Elton, 1958). The Muskrat *Ondatra zibetica* was brought from the United States to Bohemia in 1905, and after 25 years spread over an area with a radius of 180 miles, an average of eight miles per annum (Elton, *loc. cit.*). Turning to our own country, I should like to quote the following examples: The Indian Myna *Acridotheres tristis*, introduced into Durban about 1900 (Bigalke, 1936), reached Johannesburg before 1950, having made 400 miles in under 50 years which makes the rate of dispersal about eight miles per annum. The European Starling *Sturnus vulgaris*, brought to Cape Town about 1900 (Bigalke *loc. cit.*), is said to have reached Port Elizabeth in 1956 (Macnae, 1961)—an average rate of dispersal of about eight miles per annum. A similar rate of dispersal has been observed in the case of the English Sparrow. Lastly, the American Grey Squirrel *Sciurus carolinensis*, released near Cape Town in 1900, spread to an area with a radius of 40 miles by 1948, increasing its area by about 0.8 miles per annum (Davis, 1950).

The above data show how fast a species can spread when the environmental resistance is reduced or absent. Let us compare this speed—the potential rate of dispersal of species—with the periods available for the establishment of the present pattern of distribution of animals in Africa. It is usually assumed that most of the species living at present on the African continent have come to be where they now are in the course of the Pleistocene, that is during the last 1,000,000 years. The African continent is, roughly, 5,000 miles from north to south. Now, if any species spread its area at the rate of the Indian Myna or the Gypsy Moth, it would cover the whole continent in 600 years. If the dispersal were at the relatively very slow rate of the grey squirrel the continent would be fully occupied in 6,000 years. To cover the whole continent in 1,000,000 years it is only necessary to proceed at an average speed of eight yards per annum—a rate probably within the reach even of soil mites!

What emerges from these considerations is that the powers of dispersal of animals over

the surface of the earth are quite out of proportion to the time available; and that, if any of the indigenous species were capable, under existing conditions, of increasing their area of distribution, they would have done so long ago. The present pattern of distribution is therefore a *stable* one, or rather it is one of dynamic equilibrium, which is characterized by continuous attempts of animals to disperse more widely and the impossibility, under present circumstances, of getting a foothold anywhere outside their established areas of distribution. This does not apply to newly introduced species or to some indigenous species which are now moving into new environments created by man.

We must now consider the nature of the factors which contain the majority of indigenous species in their present areas of distribution. A very important and much used concept is that of "*barriers*"—obstacles which supposedly prevent the actual spread of certain animals across them. Some such barriers have been discussed in the present symposium. The most efficient barrier, it seems, is the one preventing fresh water fishes from spreading from one river system into another, even an adjacent one. This difficulty might explain the extreme poverty of the fish fauna in the southern Cape Province, although further north it is much richer, and presumably at least some of the species would have been able to live in the river systems of the southern Cape, if they could get there (Crass, p. 232, Farquharson, p. 249). Even waterfalls seem to be effective physical barriers for fish (Jackson, p. 227, Crass, p. 231). In the well documented paper by Benson, Irwin and White (p. 155) it has been shown that river valleys and rifts have served as barriers for the distribution of some species of birds. These barriers are, however, of a somewhat different kind: Mr. Irwin in presenting the paper has made it clear, that he did not suggest that birds never cross the barrier. This isolation is therefore not absolute. Evidence of the degree of isolation is provided by the existence of different subspecies of birds on the two sides of the valley. To evaluate what this means we should apply the conclusions drawn from the mathematical analysis of natural selection, worked out by Fisher, Sewall Wright, Haldane and others. Wright, in particular (1940), has calculated that, given an average level of selection pressure, genetic differentiation of two populations is not prevented by an exchange of 0.1 per cent of the population in one generation. It is thus quite possible that the subspecific differentiation has been going on in spite of a moderate gene exchange across the barrier.

In most cases of species distribution the border of the area is not delineated by any physical barrier at all: the animals are free to migrate, and the factors holding a species back are those which make it impossible for it to survive and reproduce. These factors are partly abiotic: temperature, moisture, nature (chemical and physical composition) of the soil; and partly biotic, including competition with other species. This seems perhaps elementary, but some important conclusions arise directly from the above. If animal distribution were dependent mainly on physical barriers, large numbers of different animals would have common boundaries of distribution. But if the border of the area occupied by a species is dependent on ability for survival, then each species will be fenced in in a different way. The conditions of survival are extremely differentiated for different species. Furthermore, the borders of the areas under these circumstances cannot be stable: they must be likened to a wavering line, that surges back and forth like the front in a battle, depending on fluctuations in environmental conditions and on changing population pressure inside the area. The survival of any species, depending as it does on innumerable, sometimes very subtle, circumstances, will only rarely be determined by one single factor of the environment. We have heard at this symposium (Liversidge, p. 148), that the same species of birds may be found in different habitats depending on the climate. A factor, such as vegetation, which may be limiting distribution in one combination with other factors, will not have the same effect in a different context.

Due to the intrinsic difference between species, the environment for each is not the same as for any other. The distribution pattern of any species is therefore essentially unique and

unrepeatable. Nevertheless it is true that some patterns of distribution show a closer resemblance than others. The reason is either that the one species is dependent on another, or that they are both dependent on some special configuration of environmental factors, into which a number of species fit as their organic components. If we want to make sense of distribution in animals, we must try to discern such complexes, which, naturally, must encompass the plants as well as the animals. With the maze of individual specific distributions superimposed over one another, large groupings would be easier to characterize than small ones.

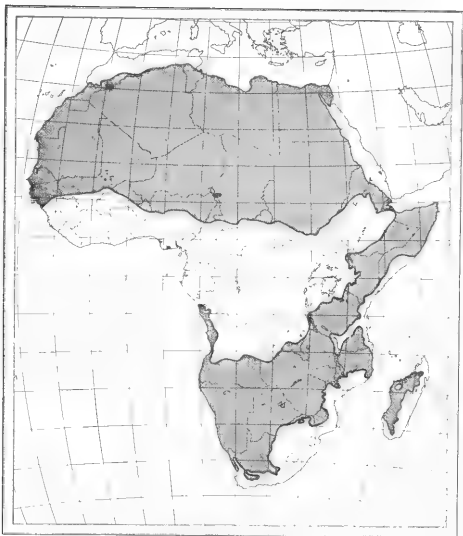
In the course of this symposium, reference has often been made to tropical and temperate components of the African fauna. Obviously "tropical" cannot be taken to mean "enclosed between the two tropics, Cancer and Capricorn". The term becomes meaningful if it is applied to a certain complex, defined by geographic, climatic and biotic characteristics. It must be recognized, at this stage, that the geographic tropical and even equatorial zones are not homogeneous in respect of climate, flora and fauna but show a differentiation in two main components. The two components are: the wet tropics, the tropics of the equatorial rain forest; and the dry tropics, the tropics of savanna merging into semidesert, as it is found in N.E. Brazil, and in Africa in Somaliland, where semidesert or desert conditions are found close to the equator. The two biotic spheres are profoundly different.

I do not have time to emphasize the difference in the conditions of life in the tropical rain forest and in the savanna, it will be enough to mention that the overwhelming majority of large African ungulates inhabit the savanna, whilst only a few large mammals, the elephant, the buffalo, and the okapi (replacing the giraffes of the savanna), are found in the tropical rain forest. The birds of the rain forest and the savanna are also, I understand, profoundly different, having but relatively few species in common.

The reason for the existence of arid zones close to the equator is not dependent entirely on the amount of rainfall, but to a large extent on the distribution of rain through the year. In the rain forest zone the rainfall is distributed throughout the year, the earth is always moist, the trees are evergreen and the animals are permanently protected from fluctuations of moisture and temperature. Towards the eastern edge of the African continent, however, the rainfall is seasonal. There is a period during which there is no rainfall, or very little. In Map I I have indicated the areas which, during at least three consecutive months a year, have less than 10 m.m. rainfall per month (the data are compiled from CCTA maps of monthly rainfall). For three months at least the zone indicated on the map is in a state of drought which may be more or less acute, depending on the absolute figures of rainfall. In this zone the trees lose their leaves during the dry season. Without the protection of the leaves, the soil is exposed to the scorching rays of the sun, and at the same time the fluctuations of temperature, annual and diurnal, become much greater than in the rainforest areas. Conditions for animal life become much more severe. From the map we see, that the drought zone extends without interruption from the western Cape and South West Africa to the Somali peninsula. The vegetation along this "drought corridor" varies from dry forest to open savanna, bush, grassland, semidesert and desert at the ends. The rainforest in the main lies west of the corridor, but on the eastern side of the continent there are patches of rainforest near the seashore and on several outcrops of mountains especially along the Rift valley.

It is obvious that the savannaland—or dry tropic—components reach far into southern Africa. The large antelopes, zebra, and giraffes are animals that thrive all along the drought corridor. The Impala occurs all the way from Transvaal (and formerly even from the northern Cape—Bigalke, p. 95) to Somaliland. To give an example for a completely different group of animals: the Neuropteran genus *Silveira* is distributed along the dry zone from S.W. Cape and South West Africa across Rhodesia to Katanga (Tjeder, 1960).

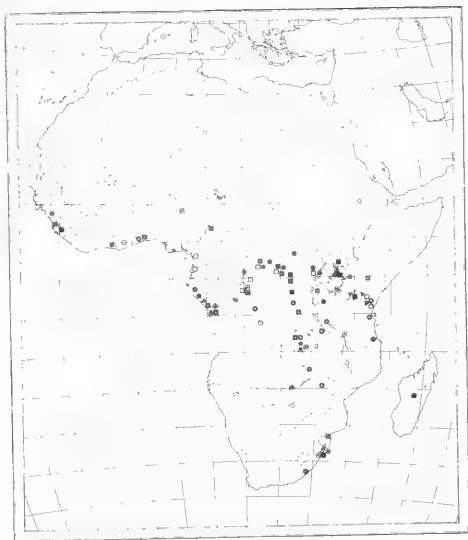
At its south western end the "drought corridor" merges into the semidesert and desert region of the Kalahari, and the Namib desert. This end of the corridor whilst closely linked



Map I. Map of Africa showing (stippled) the areas in which the rainfall is less than 10 m m. per month in at least three consecutive months. (Compiled from the CCTA maps of monthly rainfall).

to the more northern parts has developed a peculiar fauna of its own. The zone is clearly characterized by its bird fauna, as has been indicated by Winterbottom (p. 152). It has a characteristic contingent of lizards: 51 per cent of all lizards in South Africa are endemic for the south-west arid zone (Poynton, 1961); and it has 40 species of Solifugae (arachnids adapted to dry conditions) whilst Natal Zululand has seven species (Lawrence, 1953). However the most diversified and abundant component of the arid south west are the tenebrionid beetles, represented in the Namib desert by not less than 35 endemic genera with hundreds of species (Koch, 1960).

PATTERNS OF ANIMAL DISTRIBUTION ON AFRICAN CONTINENT



- | | | |
|-------------------------------|--------------------------|----------------------------|
| ■ <i>Acanthagyna africana</i> | ■ <i>A. nigritiensis</i> | ● <i>Zyxomma atlantica</i> |
| ● <i>A. bispina</i> | □ <i>A. schultzei</i> | ● <i>Z. flavians</i> |
| ● <i>A. bullata</i> | ○ <i>A. sextans</i> | |
| ■ <i>A. cylindrata</i> | ○ <i>A. unsebarica</i> | |
| ★ <i>A. flaviceps</i> | ▲ <i>A. vesiculata</i> | |
| ★ <i>A. immaculifrons</i> | ● <i>A. villosa</i> | |
| ● <i>A. manderica</i> | ▲ <i>A. nuluensis</i> | |

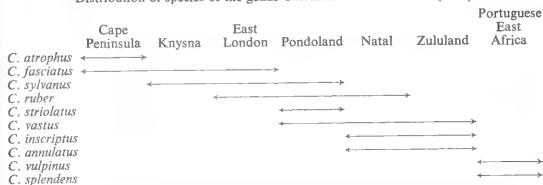
Map II. Distribution of the tropical genera of dragonflies *Acanthagyna* and *Zyxomma* in Africa.

Let us now consider the wet tropics. Do components of the wet tropics reach into southern Africa and, if so, are they related to the wet tropics to the west of the drought corridor, or only to the wet tropics along the eastern edge of the continent?

I should like to present here some data on the distribution of two genera of dragonflies, *Zyxomma* and *Acanthagyna* (Map II, based mainly on Martin, 1908–1909, Schouteden, 1934, and Pinhey, 1961). *Acanthagyna* is a circumtropical genus of dragonflies found in tropical America, East Indies, India and central Africa. The dragonflies belonging to this genus have very peculiar habits. The insects are crepuscular, fly at dusk, after sunset, and during daytime hide amongst the densest foliage. They are typical rainforest insects, though they are also found in the tropics in dense groves of bamboo (Fraser, 1949). Sixteen species are found in Africa, mainly in the Congo and adjoining territories, but also in patches of rainforest around the rift valleys and on the Indian Ocean coast. I have been able to trace three species of *Acanthagyna* to Zululand (Richards Bay) (Balinsky, 1961) and one species even as far as Port St. Johns (Balinsky, 1958). The genus *Zyxomma* has a similar mode of life, and practically the same distribution: from West Africa, through the Congo basin to Zululand (Balinsky, 1961). These data, which I know from my own experience, satisfy me that components of the western tropical rainforest fauna are in fact to be found on the eastern coast of South Africa. The distribution of other animals, in particular of the amphibians as analysed by Poynton (1960, and p. 252) fall into a similar pattern.

We are thus faced with a most interesting situation: whilst animals of the savannaland and arid areas show close relationships in a zone reaching across the continent from the south-west to the north-east, rainforest animals are distributed right across the "drought corridor" from the north-west to the south-east. It is true that in the area of the great lakes there are several patches of rain forest, mainly on mountains, which could serve as stepping stones for the movement of animals from the north-west to south-east and *vice versa*. At present, however, there are considerable areas of open country between the patches of rain forest. The difficulties can probably be explained away if we take into consideration the fluctuations of climate and the displacements of vegetation zones, as these have been indicated in the papers presented by Cooke (p. 11) and van Zinderen Bakker (p. 16). During cold and wet periods the rain forests must have expanded and closed the "drought corridor" completely or at least narrowed it still further, enabling the animals of the wet tropics to migrate from west to east (and from east to west). During hot and dry periods, the drought corridor would have expanded allowing Kalahari and even desert conditions to surge in, linking more closely the arid south-west with the Somaliland arid area, thus accounting for the close links in the fauna of these areas that have been pointed out by Winterbottom for birds (p. 152), Davis for small mammals (p. 56) and Theiler for the tick *Ornithodoros savignyi* (p. 212). The opening and closing of the "drought corridor" may have occurred repeatedly. What I said earlier on the potential rate of dispersal of animals proves that they could make full use of such fluctuations in the environment.

I now come to the last zone—the temperate zone. There is no dispute that in the south of the continent there are found numerous species, genera and even families of animals that do not occur further north. The question that we have to answer is whether these forms constitute a separate fauna, a unit which is distinct, as a whole, from the other complexes of forms on the African continent. To make this question more meaningful, I should like here to point to the very frequent occurrence of groups of closely related species distributed over a large area in such a way that either the species replace each other, or that areas of distribution of neighbouring species overlap partially. To illustrate this type of distribution I will quote the example given by Lawrence (1953) relating to species of the millipede genus *Chersastus*.

Distribution of species of the genus *Chersastus* after Lawrence (1953)

This example shows that it is dangerous to characterize faunal units by the presence of a species, without considering the distribution of closely related forms. Although, in this example, *Chersastus atrophus* would appear to be a Cape endemic, it is obvious that as a group, the species of *Chersastus* are more widely distributed; and the local differentiation in the Cape is not essential and deserves but little attention.

If it is thus desirable to check whether there is an independent temperate fauna in Africa, attention should be given to those organisms that have no closely related forms in the rest of the continent. If this criterion is made, it at once becomes evident that such a group of organisms in fact exists. Moreover, it becomes clear that these organisms constitute a distinct complex. It is the "palaeogenic fauna" that has been demonstrated in the paper given by Stuckenberg (p. 190). To this complex of animals belong some insects with aquatic larvae, such as the dragonflies of the genus *Chlorolestes*. These extend from the western Cape through the Drakensberg mountains to the Transvaal escarpment (Woodbush) and to the eastern Southern Rhodesian escarpment Inhangha Mountains. To the same complex belong the stoneflies of the subfamily Notonemouridae, the distribution of which extends as far north as the Transvaal escarpment (Woodbush). Both these groups of animals have Gondwanaland affinities. The genus *Chlorolestes* is closely related to the Australian genus *Synlestes*, and the family Notonemouridae, in addition to South Africa, is found in Madagascar (Paulian, 1949), the Tierra del Fuego in South America, and in Australia and New Zealand (Evans, 1959). I should also like to mention the frog genus *Heleophryne*, found in the Cape and in the Drakensberg mountains, a representative of the family Leptodactylidae, which is mainly South American and Australian. It is most remarkable that the tadpoles of *Heleophryne* are specially adapted to life in mountain streams. These frogs thus belong to the same biotic complex as the dragonflies of the genus *Chlorolestes*, and the Notonemourid stoneflies!

The South American and Australian affinities of the "palaeogenic fauna" have been stressed by Stuckenberg (p. 193) and of course it is known that the flora of the south Cape has the same affinities, the families Proteaceae and Restionaceae being found only in the southern hemisphere in South America, southern Africa and Australia. Affinities are also unmistakable, as is evident from fossil remains, to the Antarctic Continent.

The occurrence of common or closely related faunal and floral elements in the continents of the southern hemisphere has been one of the arguments for the existence of land connections between these continents, as postulated by the theories of continental drift (Wegener, du Toit). They were part of one whole—the Gondwanaland. The theory of continental drift had come into ill repute and had been emphatically rejected by many zoogeographers (see Darlington, 1957). In recent times, however, new facts have been discovered which put the

whole matter in a new light. The new data come from a study of so called palaeomagnetism. It appears that when rocks are being formed, either by sedimentation, or through solidification of volcanic lavas, the rocks become magnetized in conformity with the prevailing orientation of the magnetic forces at the time of their formation. If the rocks of a known age are studied, it is possible to determine the orientation of the magnetic forces during a certain period of the earth's history, and thus deduce the position of the magnetic pole at that time.

Studies of this kind have shown that the magnetic pole in ancient periods of the earth's history was not in the same position as it is now. The most astonishing fact revealed is, however, that determinations made in different parts of the world indicate different positions of the pole. This can only mean that at any given time the relative positions of the continents in respect of the magnetic poles were not the same as they are now. In other words, the continents have actually moved in respect of one another. Continental drift has actually taken place.

A weakness of the theory of continental drift has been previously that no forces were known which could account for the movement of continents. Now this fault is also being eliminated. Two major theories proposed in this connection are that the continental drift is the result of thermal convections in the earth's mantle, which underlies the continents (see Dietz, 1961), or that the earth is actually expanding, bursting at the seams as it were, the seams situated in the midoceanic ridges, with the result that ocean beds broaden, and the continents become disrupted and drawn apart (see Carey, 1958, Heezen, 1960).

From data on palaeomagnetism it is not only possible to deduce that continents have moved, but, with more abundant data available, it will be possible to reconstruct the course of their migrations and their exact positions for any period of the earth's history (Irving, 1958). I may venture a prediction that, within foreseeable future, the state of affairs in relation to continental drift will be completely the reverse of what it used to be. Formerly land connections between continents were adduced by biogeographers to explain certain peculiarities of animal and plant distribution. Now the positions of continents in the past and their movements will be established on an objective basis, as we know the duration of geological periods from uranium and carbon determinations (see Kulp, 1961), and to these data the biologist will have to adapt his theories of animal and plant distribution. It will be possible to make certain predictions. Even now it is possible to make a definite prediction as to the animal fossils which will one day be found on the Antarctic continent.

I will now return to the temperate fauna of southern Africa. It will be seen that this fauna is nothing else but the relict of the Gondwanaland fauna. As the separation of the Gondwana continents occurred presumably some time during the Cretaceous period, the common Gondwanaland elements can only belong to groups which were developed not later than middle Mesozoic. These would be various invertebrates, including arthropods and the more ancient groups of insects. Amongst the fishes the most advanced groups, such as the Cyprinids, are excluded. The frogs evolved in the earlier part of the Mesozoic (see Griffiths, 1956) and therefore could be represented. In this connection the genus *Heleophryne* may well be considered a Gondwanaland element. Modern lizards and snakes probably evolved too late to have been a part of the Gondwanaland fauna, and we have seen that they are not associated with the palaeogenic fauna, but have their centre of speciation in the south western arid zone. Amongst the mammals and birds, only the most ancient groups could have been common to the Gondwanaland continents. It has been suggested that the Ratitae, in spite of established opinion, may after all have been a group of common derivation and of Gondwanaland origin (Evans, 1958).

From what we know it appears that all Gondwanaland continents drifted mainly in a northerly direction, away from the southern pole, Antarctica being an exception, as it moved southwards to its present position (Blundell and Stephenson, 1959). It follows that the climate

over most of Gondwanaland was originally cold to temperate. The adaptation to this type of climate has been preserved to a large extent by animals and plants with southern hemisphere affinities. In Africa we have the greatest development of the Gondwanaland elements in the southernmost tip of the continent, and further north these elements are restricted to the mountain ranges where temperatures are lowered by the altitude. I believe that this is the reason of the otherwise mysterious feature stressed by Poynton (p. 252), namely that whilst degrees of moisture differentiate between animals of recent adaptation, temperature divides faunas of different historical origin. This difference is due to the past existence of the Gondwanaland continent and is not represented in the same way in the northern hemisphere where the fauna and flora of the higher latitudes is not more ancient, but on the contrary more modern than that in lower latitudes. This, of course, in its turn is due partly to Pleistocene glaciation.

In Africa the ancient temperate fauna must have occupied during early Mesozoic a considerably greater part of the continent, and at some stage the present disconnected distribution on mountain ranges may have been linked together. Nevertheless a considerable northern part of the African continent must have reached into the zone with a hotter and possibly more arid climate. The fauna of this zone seems to have merged across the equator with the fauna of *Lauasia* (the present Holarctic) and is not recognizable as a separate unit any longer. Instead it has given rise, on the broad expanses available for their distribution in the northern hemisphere, to the higher forms of life: birds, mammals, modern reptiles, amphibians and fishes, which now figure in the fauna of Africa as the dominant components of the wet and dry tropics, and even of the arid south-west.

The temperate faunal elements were prevented from merging with this stream of modern life by their adaptation to cooler temperatures and by being closely linked together in biotic complexes such as those of mountain streams and evergreen forests of the south, for which the equatorial and subequatorial zones have served through the ages as an insurmountable barrier.

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Prof. D. W. EWER
IN THE CHAIR.

Final
discussion

THE CHAIRMAN: In this final discussion we have an opportunity to compare and collate all the information presented at this meeting and to relate it to the broad scheme advanced by Professor Balinsky. In our previous discussions we have dealt with the causes and problems of animal distribution at different levels. We have considered actual distribution patterns, the factors behind these patterns and also the history and origin of the distribution. Sometimes these levels have been confused.

The matter is now open for discussion.

DR. WINTERBOTTOM: In connection with a north-east/south-west and north-west/south-east divide, Professor Balinsky has suggested that in the wetter periods the forest must have extended much further east than it does today. This is the assumption to which most workers have been driven by the facts of distribution. Recently, however, it has been much played down by others who suggest that if the forest was there at all in pluvial periods, it was only in small patches and wide dry areas must always have existed. Nevertheless one line of evidence strongly suggests that a broad band of forest did stretch from east to west. This is the degree of dichotomy which exists between the faunas of the savanna belt lying just south of the Sahara and of the savanna regions of southern and East Africa. This suggests that at some period the forest formed a barrier which savanna forms could not cross, splitting them into two groups, with isolation resulting in differentiation in some cases to the sub-specific and in others to the specific level. One example is our Cape Turtle Dove which is closely related to the Vinaceous Dove of West Africa. They were regarded first as con-specific but the weight of opinion now is that they are separate species. There are many other such cases in birds and probably other animal groups. This, in my opinion, is presumptive evidence that there was a forest barrier.

MR. STUART IRWIN: Chapin also suggests that the forest extended from the Belgian Congo through to East Africa. He argued that the distribution of the bustards and a number of other dry grassland forms pointed to separation. These forms are separated today not by forest but by moist savanna. This could well have been the case in earlier periods.

PROF. VAN ZINDEREN BAKKER: When we talk about forest I think we must draw certain distinctions, as there have been different types of forest. If we are to consider the heavy traffic

of animals up and down Africa, suggested by Professor Balinsky this morning, we must also postulate open routes. During the cold periods, that is, the more humid or hypothermal periods, there may not have been so many routes. On the central plateau a wetter type of savanna might have prevented movement north and south. On the escarpment and mountain areas there would have been a mountain forest: and, along the east coast, tropical rain forest of which at present there are relics. During a hypothermal period, therefore, there would not have been such possibilities for traffic by dry species. During the drier periods, or non-pluvials, however, we have heard that there was a corridor going from the south-east to the north-west: and I myself have found some evidence of such a corridor at the southern tip of Lake Tanganyika. On the other hand, I would like to suggest the possibility of a coastal migration route. I wonder whether, during dry periods, we did not have much more open savanna country all along the east coast from, say, the Horn of Africa to Zululand.

MR. STUART IRWIN: My only reason for arguing against a dry coastal belt is the present existence of a rich and varied wood coastal avifauna, which could not have existed in dry savanna. Possibly, however, this fauna migrated across the plateau. We know that the fauna associated with Broken Hill man included oryx which are typical of the south-western Somali arid areas and also long-horned buffalo, which are probably open grassland animals.

DR. STUCKENBERG: Students of relict insects agree with the view that the forest extended across the African plateau. As far as the age of the African forest is concerned, various authorities are of the opinion that the forest in the Usumbara Mountains is of Miocene origin, basing this belief on the distribution of beetles.

DR. BIGALKE: The corridor theory is also supported by mammal and bird distribution. Benson and others produced a paper on birds in Salisbury last year in which they quoted a number of examples of pairs of closely related species or subspecies showing a gap in distribution from the north-east to the south-west. Amongst mammals the oryx shows this pattern clearly, with one species in the northern area and another in the southern region, ranging as far as Bechuanaland. There is also a record of Springbok remains in Olduvai Gorge; and the dameliskines show this type of distribution too.

DR. WINTERBOTTOM: I myself have no quarrel with a suggested route across this area which at the present moment consists of a band of savanna. However, the species pairs to which I originally referred, are not distributed north-east south-west and the barrier for them does not seem to be moist savanna. For instance, the Cape Turtle Dove goes right through the moist savanna and it and the Vinacious Dove meet somewhere near Uganda. Thus no barrier exists at present.

DR. BRAIN: From a purely geological point of view there is very good evidence for a dry corridor in the distribution of Kalahari type sand, as mentioned in Dr. Cook's paper. These sands extend from the Kalahari north to the Congo, strongly suggesting a dry corridor in one of the interpluvial periods.

DR. STUCKENBERG: Could I ask Dr. Brain for his views on the date of the sands?

DR. BRAIN: The dating of such sand is very difficult because in effect the sand has always been there; it is immensely old. Thus it is really a matter of dating the redistribution, which probably happened on several occasions during the Pleistocene. The last major redistribution was immediately before the Gamblian period, say 50,000 to 100,000 years ago.

THE CHAIRMAN: We seem to have reached agreement on the existence of a dry corridor, but other questions remain. There is for instance, the problem of an archaic fauna which is so clearly shown in the arthropod groups; and we also have the question of a temperate fauna specific to the Cape. Is this temperate fauna an archaic one or has it come down from the tropical zone and re-adapted to the cooler area? I am thinking, for instance, of the widely distributed genus *Xenopus* which has temperate and also tropical species. Dr. Poynton suggests a temperate amphibian fauna but I do not know how this would relate to Gondwanaland. Perhaps Dr. Poynton would like to say something on this matter.

DR. POYNTON: There is one group which might throw some light on this, namely the genus *Heliophryne*. The group is most prominently found today in Australia and South America and there is an Eocene fossil from India, which must be post-Gondwana. This could possibly represent a Gondwanaland distribution or it might simply mean that the group was originally world-wide and has just been left in isolated regions. On the whole, I think that Darlington is right here, particularly in regard to the vertebrates, in leaving out the Gondwana story. As you know, he did not reject it entirely, but said it happened far too early to affect vertebrate distribution. In the case of the amphibia in the south-west Cape, there is no definite indication that any of the forms are from a Gondwanaland fauna. All could be derived from an earlier world-wide fauna, now restricted to certain areas, and now to be regarded as a temperate fauna, (a) because of its distribution pattern, and (b) its phylogeny. As with the north temperate fauna, there is a pronounced ancient element in the south-west Cape with a mixing of very old families and more modern groups.

PROF. BALINSKY: As the break-up of the continents occurred in the late Mesozoic, it is obvious that any remaining elements of a Gondwana fauna must have evolved before this time, in the first half of the Mesozoic. This is why the Gondwanaland fauna is mostly restricted to invertebrates, such as the more archaic arthropods, including the more ancient group of insects, and it would logically include the older fishes; but apart from *Protopterus*, the status of the Dipnoi is not very clear. Amongst the amphibia the frogs seem to have developed in the early part of the Mesozoic, so it is quite possible for them to have been a part of this Gondwana fauna, particularly *Heliophryne*.

I would like to point out an interesting ecological consideration. We know the tadpoles of *Heliophryne* are adapted to fast running mountain streams, and that is exactly the type of environment in which we find the palaeogenic insect larvae, the stone flies, and so on. This gives a fairly strong indication that this amphibian might be a relict of the Gondwana fauna. The fact that Leptodactylid frog remains have been found in India, is also a strong indication of this. As for reptiles, these are represented in South Africa by lizards and snakes which are more recent than the early Mesozoic. The mammals and birds could only be represented by more ancient forms amongst which the Ratitae may prove to be a Gondwana element. One suggestion of this is that, according to Professor Leymans the African ostrich and the South American ostrich have identical bird lice. Amongst the mammals of Africa, there seem to be two distinct strata, the ancient forms such as the Aardvark, the Scaly Anteater and the mongooses, and the more modern types, such as the large ungulates and the carnivores. There does not seem to be enough substance to prove that the edentate-mongoose fauna, if I might call it that, is a Gondwanaland element, although there are similarities to the South American fauna.

DR. POYNTON: Professor Balinsky's point about *Heliophryne* being found in running water is a very interesting one. However, many relict forms show a similar tendency, a preference for this type of environment. Furthermore, the fossil Leptodactylid which has been

mentioned is from the Eocene of India and could well point to a world-wide distribution of the family rather than a Gondwana distribution.

DR. OMER COOPER: No one has so far mentioned *Phreatoicus capensis*, a small crustacean living in pools in running streams. This animal has never had a world wide distribution as far as we know. Our species is variable but not divided into clearly defined forms and it extends all along the Cape sandstone zone on the sea side. A fossil species very closely allied in structure is found in Australia, and in New Zealand there are a dozen or so related genera and perhaps fifty species. Recently a species very near to *Phreatoicus* was found in India, and is being worked on and compared with our material at present. For various reasons this seems to be a good example of a Gondwana animal: it cannot fly; its eggs cannot be carried on the feet of birds because the female carries them; it also cannot be blown in the wind; and it dies in sea water.

DR. PLUMSTEAD: I think that one or two bits of geological and palaeo-botanical evidence on Gondwanaland may be of interest to zoologists. Recently I have been working on the fossil plants of Antarctica, and these are similar to those of the Cape from the lower Devonian and Bokkeveld. The coal plants from the late Carboniferous and the early Permian and Triassic plants are similar to those of our Molteno and lower Jurassic, and closely comparable to those of the older parts of Gondwanaland. It would appear that Africa broke away at the end of the Jurassic. Further Africa seems to have broken away first, and to have moved northward. A cold temperate flora developed in the rest of Gondwanaland including *Motophagus* and *Auracius* which were common to South America, the Falkland Islands, Australia, and even India. So there should be a faunal tie-up of animals that were common to Africa up to the late Jurassic, and not common after that time.

DR. STUCKENBERG: Dr. Plumstead's account seems to tie up in many different ways with the distribution of invertebrates, in particular with those paleogenic groups which live in cold mountain streams. There are very few of these in South Africa compared to the tips of other continents. Australia, New Zealand and South America have many more and they have many more in common with one another than they do with South Africa. This would make sense, following Dr. Plumstead's remarks.

A curious thing about these elements in South Africa, is that their affinities lie almost invariably with Australia, Tasmania and New Zealand and not with South America. This is a well marked feature and it is really quite an event to find a paleogenic animal related to South America.

PROF. WELLS: I would like to return to a point made by Professor Balinsky about the older and younger strata in the mammalian fauna of South Africa. We may perhaps call these the pre-Miocene and the post-Miocene strata, the first consisting of generally archaic forms derived from rather unspecialized groups (although they have produced some very specialized representatives, as among the insectivores, for instance), and the second, post-Miocene strata consisting especially of the dominant ungulates. But I would like to suggest further that there were probably several levels within these major divisions, especially in the post-Miocene group. Among the antelopes, we can possibly recognize earlier and later elements, in the sense that there are certain antelope groups which have always been confined to Africa (the Duikers and the Neotragines, for instance), whereas the other antelope groups have included Eur-African and Eur-Asiatic members. During the later Miocene and Pleistocene they gradually became narrowed down to Africa. From that, I would like to go on to tie up with what I think was Dr. Winterbottom's original point about distribution in Africa,

because one particular group, the Hartebeest, illustrates his point very well. We have a belt of related species of Hartebeest (some people say only sub-species), crossing the savanna belt south of the Sahara with some differentiation from west to east and we have what appears to be a reasonably closely related form, the Red Hartebeest in Southern Africa. Interposed between the two, we have the quite distinctly divergent Lichtenstein's Hartebeest.

We do not know enough about the paleontology of these animals to work up a theory as to how this differentiation has come about, but we are aware that during the early Pleistocene, there was an extraordinary accumulation of Hartebeest-like fossil antelopes in southern and East Africa. In fact, there were probably twice as many genera and species as we have in the later Pleistocene and Recent. Possibly as we get to know these forms better, some theory will emerge.

DR. WINTERBOTTOM: I should like to make one small comment about the Ostrich and the South American Rhea. In the Tertiary, the Ostrich was not confined to Africa, but was found in central Asia as well. If it was a Gondwanaland relic, it must have got out of Gondwanaland and have spread into what is now the whole Arctic region. This does not necessarily invalidate the suggestion that the Ostrich and Rhea may be Gondwanaland relics, but it is perhaps a modifying factor.

PROF. BALINSKY: I don't think this is a contradiction because the Ostrich has obviously emancipated itself from the complex of temperate forms and gone over into the tropics, at least the dry tropics. Then, of course, its limit of distribution was the end of the northern continent with which at that time Africa must have had a connection.

THE CHAIRMAN: We seem to go constantly back to Gondwanaland and I want to put my problem once again. I don't really feel that Dr. Poynton clearly answered the question. He spoke of the possibly Gondwana origin of some amphibia, but I would like to know whence come the non-Gondwana-elements in the south temperate fauna of the Cape today. Do they have a tropical origin or was there at some earlier period a connection with the north-temperate fauna? The fact that the northern-temperate regions and the southern temperate regions show similar constitution, seems to me to provide a problem which lies somewhere between Gondwanaland and the more recent period. Are you willing to answer this, Dr. Poynton?

DR. POYNTON: Here I follow Darlington, believing that the world fauna as a whole emerged in radial waves of distribution from tropical regions, more particularly those of Africa and India; and with these waves there were movements to more unfavourable areas, both north and south. I think the Amphibia provide very convincing evidence for postulating such waves, and also for supposing that before one wave has reached the final backwater—let us say in South America—the next wave is on the way already. I would therefore say that the fauna of the South-west Cape has been derived from the northern equatorial areas and this fairly recently. By now these forms have been ousted from equatorial regions by new forms, but they are still preserved in extra-tropical areas. The distribution of *Heliophryne* can be explained in this way, and I think the theory probably holds good for the vertebrates as a whole.

DR. WINTERBOTTOM: There is one point about Darlington's theory which might be elaborated a little because it is an aspect which is not always clearly understood. Many workers believe that this theory postulates a general pattern of distribution and succession whereby the primitive forms get pushed out to unfavourable environments and left there, while the highly evolving centres contain the newest forms. However, Darlington himself in, I think,

his most recent paper has pointed out that this is by no means the invariable rule. On the contrary, very many primitive forms remain in the tropical areas after they have died out in more temperate regions and Darlington explains the extraordinary richness of the tropics by saying that they include:

- (a) newly evolved forms which have not had time to spread outwards as yet;
- (b) forms that have already spread over the temperate and the tropical areas;
- and (c) more primitive forms which have been extinguished in the temperate zones but have managed to find a niche to hang on to in the tropics.

MR. STUART IRWIN: I would like to point to a group that is abundant in your Cape region but that does not appear to be a relict. I refer to the genus *Serinus*, an abundant one, not only in species but also in individuals. Further north in the tropics, the serins are replaced by weavers and waxbills. Both groups are basically rather similar in habits, both are equally advanced, and yet one excels in a temperate climate and one in a tropical. Here then we have in the serins a group which could be taken as a relict (but I personally do not think it is), and they have relatives in the Palearctic, and the Nearctic and many species throughout the rest of Africa, especially on the mountains.

DR. WINTERBOTTOM: The Fringillidae are essentially a temperate group because there are, in addition to a few widespread species in tropical Africa, others which occur in the tropics but only in the temperate parts of it, that is to say, on the mountain tops. They are the most numerous, I think, of all the Passerine bird families. They have more species in the whole Arctic region than any other Passerine family and they are also extremely abundant in North America.

PROF. WELLS: I would like to put a question which I hope Dr. Plumstead will be able to answer for me regarding the geological history of Africa.

I seem to recollect, having heard it said on an earlier occasion by Dr. Cook, that there has been a great deal of up-warping of the African continent in the latter Tertiary, since the Miocene, and that there has been an elevation of some thousands of feet in inland plateau areas. It seems to me that, if that is the case, it must have effected quite considerable changes in the climate of the continent and it may well have upset our distribution area quite considerably as compared with the early Tertiary. It may also have had the negative effect, which bothers us so much, of preventing any deposition of Pliocene deposits.

DR. PLUMSTEAD: Professor Wells' point about up-warping is of very great importance in the preservation of fossil life right through Africa's history. Professor Holmes of Edinburgh has recently published a map in which he shows that Africa has always had what he calls "a basin and a swell" structure: a series of basins separated from one another by high connecting ridges. This characterizes the structure from pre-Cambrian times. For the fossil record, this is extremely important because, even in periods of uplift, Africa has never been a crumpled area. The whole region has in fact, been subjected to movements upward and downward, and not to orogenic movement, except in the Atlas mountains and the Cape fold belt. The basins have preserved some remnants for us even on the highest portions. Apart from them the continent would have been scoured down to its granite basement throughout instead of just in patches.

DR. STUCKENBERG: Perhaps I may venture some comments too. A very significant feature in the geological history of Africa is the complete reduction to a peneplain by the end of the mid-Miocene. Various estimations have been made as to the elevation of this peneplain.

These are generally rather low but I have seen one calculation which gives the maximum elevation at 2,000 ft.

To go back to Professor Wells' question: this peneplain has been elevated at least three times, the first elevation occurring in the mid-Miocene, the second in the Pleiocene and the third in the Pleistocene. There seems no agreement between various authors as to the extent of the elevation on each occasion. Probably the greatest extent of African forestation was achieved at the close of that planation in the mid-Miocene. It seems possible to me that this offers a not unreasonable explanation of the distribution of mammals or at least the ungulate mammals.

MR. GRINDLEY: I would like to return briefly to the point made by Professor Omer-Cooper, regarding the crustacean *Phreatoiculus*. I think we have to be very careful here about suggesting that these little crustaceans were limited to the Gondwana area. There is for instance another similar genus, *Protojanira*, which now has three species found in South Africa in the mountains of the south-west Cape and in the Drakensberg; and there are forms fairly close to this which are found widespread in the deepest oceans. It seems clear that these forms are relicts of a primitive group and it seems that the distribution of these groups was once far more widespread than merely the Gondwanaland continent. The absence of fossils of forms as small as this is not a good indication that they were not more widespread in earlier times.

THE CHAIRMAN: Professor Balinsky mentioned the importance of barriers in the development of species and the limiting of gene flow; and one of the questions which seemed to me to have been little discussed is the dynamics of speciation. I wonder if there is anyone who has any feelings to express about this and also of the importance or otherwise of trying to recognize generalized climatic or biotic factors determining distribution.

DR. POYNTON: As regards speciation, there is a point which might be brought to the attention of workers in Africa studying distribution. This is the work of Brown in America, on what he calls centrifugal speciation. I do not know whether the members of this gathering are familiar with his paper which appeared some two years back. It seems that we have in this country enormous scope for studying the problem of centrifugal speciation in that we have an apparently robust centre of speciation in Central Africa. The limits of this centre are clearly marked by some quite marked changes in climate which cause an expansion and contraction in the tropical fauna and flora, producing conditions most favourable for the development of species at the periphery, as opposed to the more generalized changes which take place—or are supposed to take place—in the central area. I have no information myself which might contribute to Brown's idea but I think the attention of workers could be drawn to this very interesting theory.

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